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The factors governing shape and size in Capsicum fruits; a genetic and developmental analysis[1]

SAMUEL KAISER

(WITH SEVEN FIGURES)

INTRODUCTION

Living things, and the parts which constitute them, are generally characterized by a definite form and magnitude, capable of relatively slight modification by a varying environment. The diversity of shape and size among plant and animal groups, and the relative constancy of these features within a species or variety, indicate that these characteristics have a definite genetic basis. This has been proved experimentally in a number of cases. In most of these, shape and size seem to be inherited as are most quantitative characters and governed by the action of multiple factors, but in several instances it has been shown that each may be controlled primarily by the action of single genes.

An attempt is made in the present paper to ascertain the genetic mechanism of shape and size determination in the fruits of *Capsicum annuum*. The problem has previously been studied, with results which seem to the writer to be inconclusive. Webber (1912) has reported a cross involving parental fruit types of different size in which the F_1 was intermediate and the F_2 distribution was continuous, being skewed toward the large end. Ikeno (1913) obtained an intermediate F_1 in such a cross also and found in the F_2 a graded series ranging from the size of the large parent on the one side to that of the small parent on the other. His results indicate that the parents differed in four or five size factors. Halsted (1914, 1915, 1916), however, failed to recover the parental types in an F_2 progeny of 1000 plants, indicating that more size factors were here involved. Shape in his material likewise showed a typical "quantitative" inheritance. Groth (1915), having carried out an extensive investigation on tomato fruits, published a plate of pepper fruits (without accompanying analysis) which shows a wide variety of shape and size types in the F_2. Castle (1923) has used such a plate in support of the thesis that size and shape do not have a simple genetic basis, saying, "It is evident that in these cases length and width of the fruit are affected by numerous independent factors which recombine so as to form a complete series of inter-

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grading forms." Dale (1928) has presented evidence for the proportionate effect of a number of quantitative factors controlling fruit length. The most exhaustive study of quantitative characters in this species has recently been made by Deshpande (1933). According to this author, "Length of fruit is probably inherited on a tri-hybrid basis in the ratio of 3 short and intermediate fruits to 1 long." "Thickness of fruit" (the equivalent of width in the present study) "is inherited on a simple monohybrid ratio." With respect to fruit shape, elongate and globose being the contrasted types, "F_1 had partly taken both the characters, one from each parent," and "this character is influenced by a large number of factors." There is thus in this series of findings much that is contradictory. Related work on other organisms will be discussed later in connection with the results obtained from the present investigation.

The analysis which follows will endeavor to establish two main points: (1) that shape and size of *Capsicum* fruits are inherited *as such* and not merely as the resultants of independently inherited linear dimensions, and (2) that the final shape of the mature fruit is genetically determined by the interaction between factors governing the *relative* dimensional growth rates during the course of the organ's development and factors controlling its *absolute* size.

MATERIAL AND METHODS

A number of commercial varieties of the red pepper, *Capsicum annuum*, were inbred for several generations to insure a fairly complete degree of homozygosity, and then crossed. The varieties chosen as parents were those between which there were obvious differences in mature fruit shape and size, and which could be successfully grown in pots in the greenhouse. F_2 generations were grown from several of these. Of the many hybridizations performed four were selected for intensive study, two of which are here reported as examples of two different types. In the cross between Lines VIII and V, the parental fruit types are more strikingly contrasted in shape than in size. The fruits of both types are small. Those of Line VIII are long and narrow, tapering toward the stigmatic end. The fruit is characteristically made up of two carpels and the pericarp is rather thin. At maturity, the placenta bearing the seeds occupies only the basal portion of the berry. In Line V, the fruits are flattened spheres, the apices being blunt. They are usually bicarpellary and the pericarp is thin, but somewhat thicker than in Line VIII. At maturity, the entire berry is filled with seeds. In the cross between Lines IV and IX, the parental fruit types are more extremely contrasted in size than in shape. The mature fruits of Line IV are much larger than those of Line IX and somewhat more

elongate, although not pointed. The number of carpels is variable but is generally two and the pericarp is rather thick and fleshy. Seeds are found only in the basal portions of the mature fruits. Line IX seems to be genetically very similar to, if not identical with, Line V.

Ripe fruits of the parent, F_1 and F_2 plants were measured with vernier calipers and the measurements studied statistically as outlined in the following pages. Length is always measured, in centimeters, as the linear distance from the junction of the ovary base with the receptacle to the ovary-style fusion. Width, in centimeters, is the maximum width of the ovary. The fruits are radially symmetrical, width in all directions being essentially equal. Volume is computed according to the arbitrary calculation width^2×length and is expressed in cubic centimeters. (These computed volumes are obviously larger than the actual volumes; they may be conveniently employed, however, as comparative size values.) Shape index is calculated by dividing the longer of the dimensions by the shorter; but in order to facilitate the statistical work, all the shape indices are expressed

TABLE 1

Summary of statistics in the VIII×V cross. The numbers in parentheses indicate the number of measurements involved.

		VIII (21)	V (60)	VIII×V (36)	F_2 (70)
Length cm.	$\bar{m}$	6.87±0.09	1.34±0.01	3.74±0.06	4.60±0.10
	s.d.	0.64±0.07	0.17±0.01	0.58±0.05	1.28±0.07
	v	9.38±0.99	12.60±0.79	15.37±1.25	27.93±1.71
Width cm.	$\bar{m}$	1.46±0.03	1.83±0.02	1.75±0.02	2.13±0.03
	s.d.	0.18±0.02	0.19±0.01	0.21±0.02	0.36±0.02
	v	12.46±1.32	10.53±0.66	12.21±0.99	17.00±1.00
	r, L-W	+.41± .12	+.67± .05	+.24± .11	−.48± .06
Shape L.	$\bar{m}$	4.77±0.10	0.73±0.01	2.16±0.04	2.27±0.07
	s.d.	0.66±0.07	0.07±0.00	0.37±0.03	0.86±0.05
	v	13.79±1.46	8.95±0.56	17.21±1.41	37.72±2.44
Volume c.c.	$\bar{m}$	14.97±0.67	4.59±0.11	11.78±0.40	20.41±0.55
	s.d.	4.59±0.48	1.31±0.08	3.57±0.28	6.80±0.39
	v	30.64±3.48	28.60±1.90	30.28±2.62	33.30±2.10
	sk				+0.45
	r, S-V	−.45± .12	+.10± .09	−.04± .11	+.03 ±.08
Volume log.	$\bar{m}$				1.289±.013 (antilog: 19.46)
	s.d.				.155±.009
	v				53.63±3.83
	sk				+0.01

in terms of relative length (length divided by width). The advantages of employing shape indices of the former type have been pointed out elsewhere (Sinnott, 1927).

In addition to the study of mature fruit dimensions, those of developing fruits were measured, from young ovaries of .001 c.c. or less in volume to mature fruits of 100 c.c. or larger. This developmental study, which provides a method of analysis not realized by the conventional work with mature fruit dimensions, has an important bearing on genetic interpretations.

STATISTICAL ANALYSIS OF MATURE FRUIT DIMENSIONS

The results of both crosses will be considered together. The frequency distributions for length, width, shape, and volume are given in figures 2, 3, 5, and 6. Summaries of the statistics, including the means ($\bar{m}$), standard deviations (s.d.), coefficients of variability (v) in percent, coefficients of skewness (sk) (for F_2 volumes only) and coefficients of correlation (r)

TABLE 2

Summary of statistics in the IV×IX cross. The numbers in parentheses indicate the number of measurements involved.

		IV (4)	IX (61)	IV×IX (50)	F_2 (105)
Length cm.	$\bar{m}$	6.28±0.20	1.26±0.02	1.86±0.02	3.39±0.07
	s.d.	0.58±0.14	0.20±0.01	0.26±0.02	1.08±0.05
	v	9.25±2.23	16.30±1.02	13.94±0.96	31.98±1.63
Width cm.	$\bar{m}$	4.48±0.06	1.82±0.02	2.49±0.03	3.53±0.03
	s.d.	0.18±0.04	0.23±0.01	0.35±0.02	0.45±0.02
	v	3.99±0.95	12.52±0.78	13.98±0.96	12.84±0.61
	r, L-W	−.27± .31	+.81± .03	+.75± .04	+.16± .06
Shape L.	$\bar{m}$	1.41±0.05	0.69±0.01	0.75±0.01	0.97±0.02
	s.d.	0.15±0.04	0.06±0.00	0.08±0.01	0.32±0.01
	v	10.75±2.59	9.16±0.56	10.15±0.69	32.72±1.68
Volume c.c.	$\bar{m}$	125.73±4.38	4.37±0.15	12.08±0.43	43.45±1.22
	s.d.	12.98±3.10	1.69±0.10	4.52±0.30	18.50±0.86
	v	10.32±2.49	38.59±2.69	37.40±2.85	42.56±2.31
	sk				+3.08
	r, S-V	+.40± .28	+.34± .08	−.13± .09	+.52± .05
Volume log.	$\bar{m}$				1.599±.013 (antilog: 39.72)
	s.d.				.190±.009
	v				31.72±1.61
	sk				−0.26

between length and width, and between shape and volume together with their probable errors, are offered in tables 1 and 2. (The loss of most of

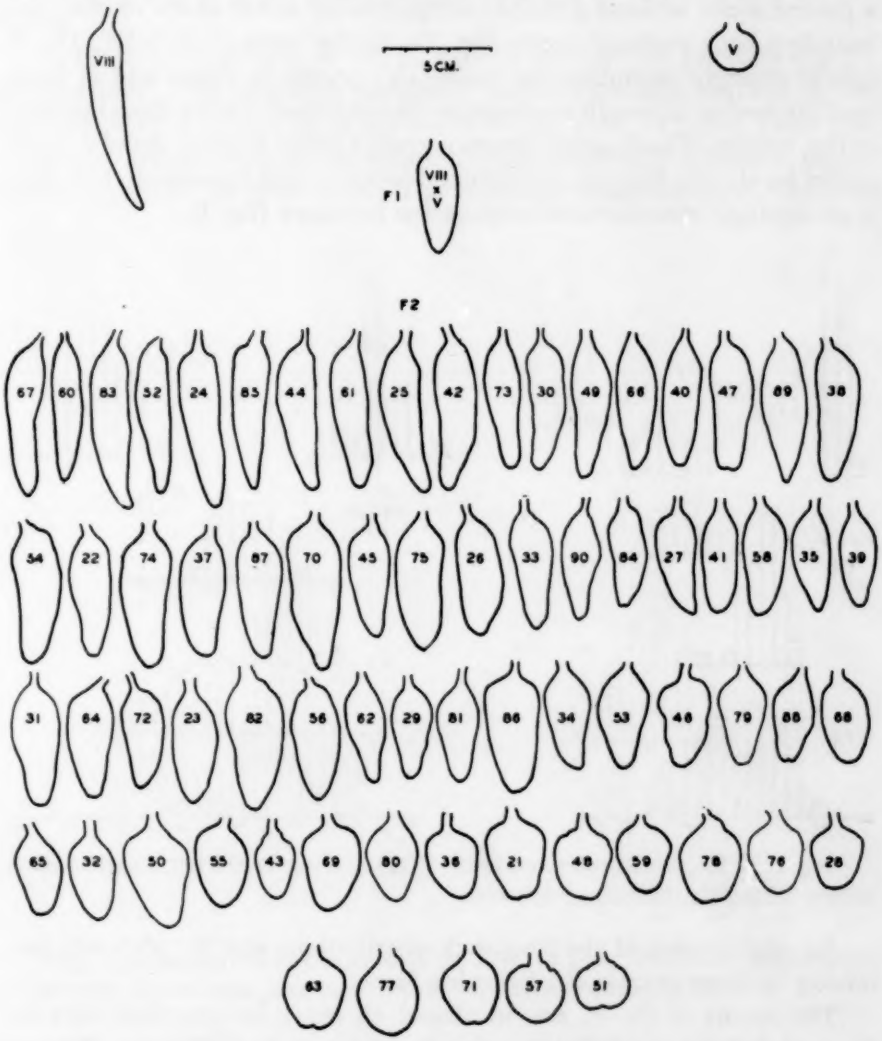

Fig. 1. Trace drawings of typical ripe fruits from the parent plants, VIII and V, the F_1 hybrid between them, VIII $\times$ V, and each of the 70 F_2 plants (numbered 21–90) these arranged in a series from the relatively longest to the relatively widest.

No clear segregation in shape is observed.

the ripe fruit measurements for Line IV has made it necessary to work with only four fruits. The statistics based on these, especially the variabilities and correlations, are of course of little value.)

In the cross of VIII×V, the F_1 hybrid is intermediate in shape and size, resembling perhaps the female (VIII) parent more strongly. The F_2 shows a graded series without definite segregation for either shape or size, and including both parental types (fig. 1). In the cross of IV×IX, the F_1 hybrid strongly resembles the male (IX) parent in shape and is intermediate in size, although more nearly like the small parent than the large in this respect. The F_2 again shows a graded series without definite segregation for size (in this case the parental types are not recovered), but there is an apparent monofactorial segregation for shape (fig. 4).

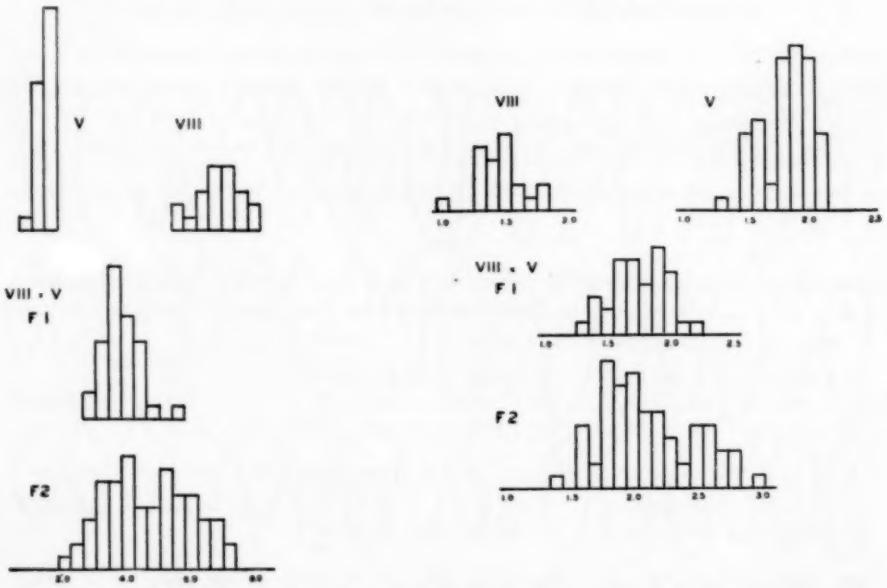

Fig. 2. Dimension distributions in the VIII×V cross. To the left, length in centimeters; to the right, width in centimeters.

An examination of the frequency distributions and the statistics pertaining to them reveals the following facts:

The means of the F_1 are, in almost all cases, intermediate between those of the parents, indicating absence of complete dominance. There is an apparent partial dominance of the male parent in length, shape, and volume in the IV×IX cross. It will be shown later that the dominance in shape is a valid one traceable to the dominant effect of a single gene in development. The dominance in length and volume seems not be very significant, as is indicated by subsequent considerations.

The F_1 means are approximately equal to those of the F_2. The discrepancies which arise (in some cases the F_2 means are larger than those

of either parent) are probably to be explained by the fact that the F_2 plants were grown in the field under more favorable conditions than the others.

In general, variability in the F_2 exceeds that of the parental and F_1 distributions. This increased variability is not especially marked in the volumes of both crosses or in the width of the F_2 of IV×IX. These discrepancies are traceable to the unusually high variability of size for plants grown in pots in the greenhouse. The increased variability of F_2 distribu-

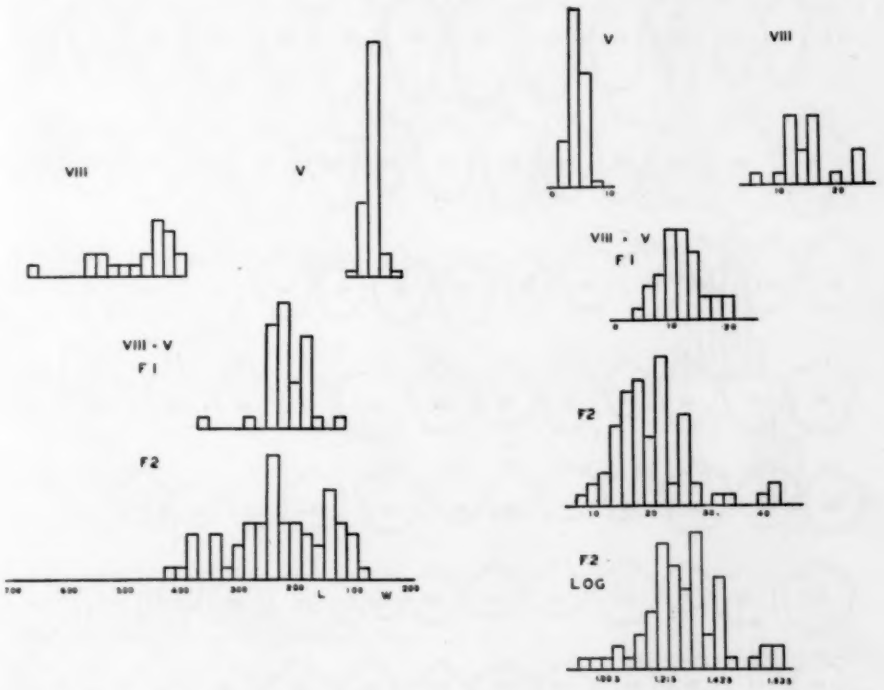

Fig. 3. Shape and size distributions in the VIII×V cross. To the left, shape index; to the right, volume in c.c., and below, the F_2 volumes plotted logarithmically.

tions has generally been interpreted as meaning that a number of genes are assorting and recombining. The question of what the genes directly control, however, has not been at all clarified thus far.

The present evidence supports, for this species, the conclusion of Sinnott (1935) for *Cucurbita* fruits, that genes control shape and total size (volume) rather than particular dimensions. This conclusion was based on the facts that (1) a simple, clearly segregating fruit shape difference is inherited independently of fruit weight (size); (2) there is rarely or never

a significant correlation between fruit weight (size) and fruit shape index in the F_2; (3) shape indices segregate much more sharply than do dimen-

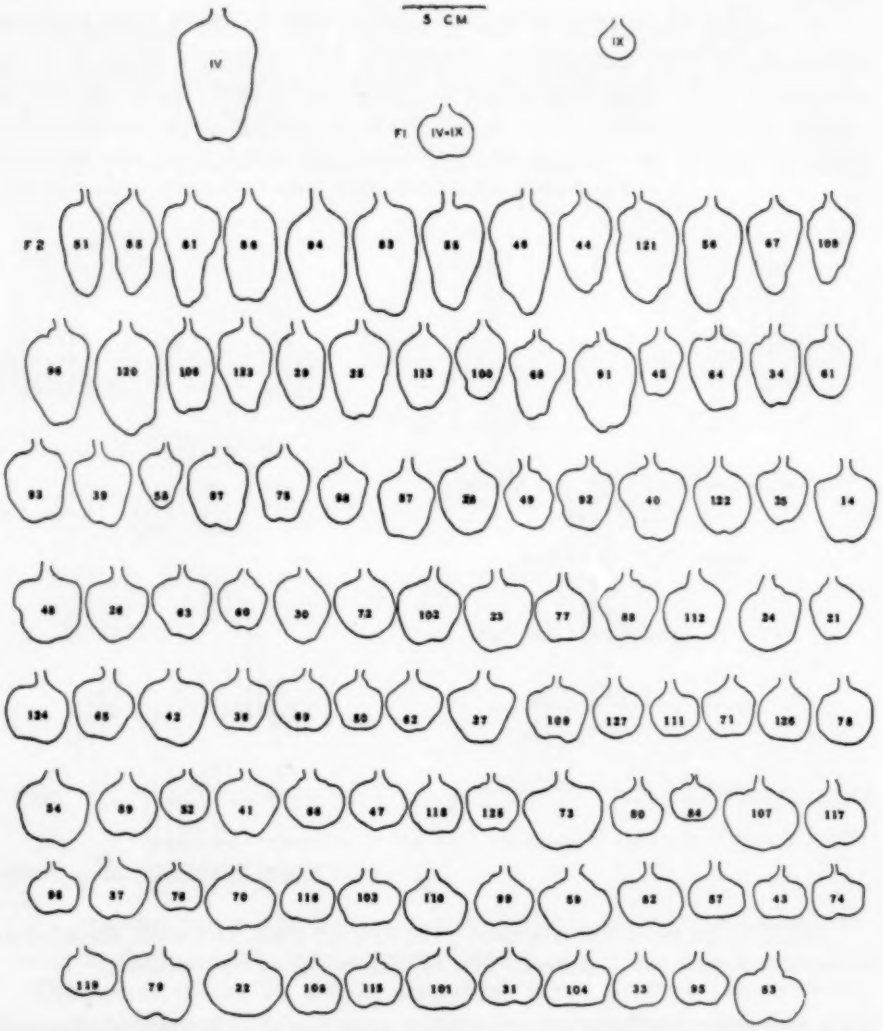

Fig. 4. Trace drawings of typical ripe fruits from the parent plants, IV and IX, the F_1 hybrid between them, IV × IX, and each of the 105 F_2 plants (numbered 21–127), these arranged in a series from the relatively longest to the relatively widest.

Note the monofactorial segregation for shape.

sional traits; (4) there is a positive correlation between fruit length and width in pure lines and F_1 progenies, but a negative correlation between these traits in the resulting F_2 progenies; (5) variability of length is twice

as great as that of width in F_2 generations from crosses between lines which differ in fruit shape, although length and width are essentially equal in their variability in both pure lines and F_1 progenies.

From the present results, it is evident that point 1 is supported by the IV×IX cross but not by the VIII×V cross (figs. 6 and 3). Point 2 is supported by the VIII×V cross (the correlation is only $+.03 \pm .08$), but not by the IV×IX cross, for the correlation here is $+.52 \pm .05$, that is, the larger fruits are in general the more elongate ones. Point 3 is sup-

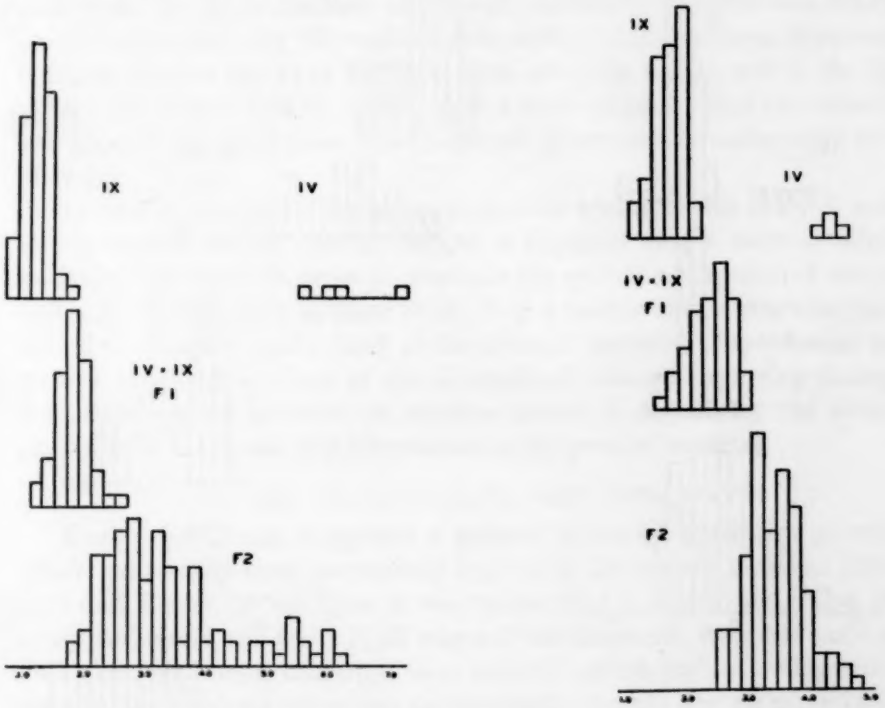

Fig. 5. Dimension distributions in the IV×IX cross. To the left, length in centimeters; to the right, width in centimeters.

ported by the IV×IX cross, but not by the VIII×V cross (see distributions in the figures). Point 4 is supported by both crosses (in the F_2 of IV×IX this correlation is not negative, but is not a significant positive correlation: tables 1 and 2). Point 5 is supported by both crosses (see summaries of statistics).

Thus the present evidence can be interpreted most simply on the basis that genes controlling shape and total size (volume) are operative and that particular dimensions are merely the resultants of the interaction of these.

A genetic analysis of shape, relatively simple in the cross of IV×IX, is very complex in the cross of VIII×V. The positive correlation of shape index with size in the cross of IV×IX suggests a linkage between genes governing size and shape, similar to that reported by Lindstrom (1928) for certain tomato fruits.

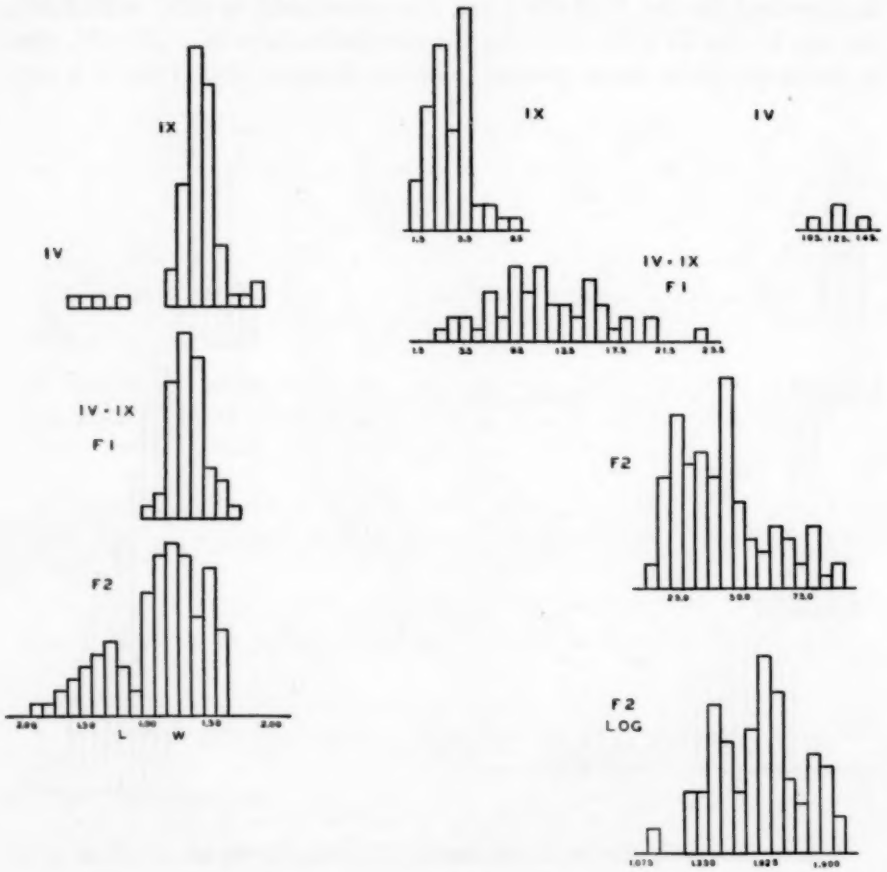

Fig. 6. Shape and size distributions in the IV×IX cross. To the left, shape index; to the right, volume in c.c., and below, the F_2 volumes plotted logarithmically.

With regard to the inheritance of size, the data are not conclusive. One obvious reason for this is the inadequate number of measurements; another, the non-uniformity of environmental conditions; a third, the rather extreme variability of fruit size even under the reasonably well-controlled conditions of the greenhouse. The results are best explained on the multiple-factor hypothesis by assuming a number of genes controlling

by their interaction the final size of the fruit. This number must be fairly small in the VIII×V cross, since the parental types were recovered in an F_2 progeny of only 70 plants. In the IV×IX cross the number is evidently larger.

The question arises as to whether the genes controlling size act additively with partial dominance or geometrically without dominance. The logarithmic treatment of growth data as advanced by Zeleny (1920), Dale (1928) and others has here been applied. The diagnostic feature in this respect is the normalization of skewed arithmetic distributions when plotted logarithmically. Normalization is striking in both crosses, skewness being reduced in the F_2 of VIII×V from +0.45 to +0.01, and in the F_2 of IV×IX from +3.08 to −0.26. Such a result suggests that the several size genes involved in these crosses operate geometrically rather than additively.

In view of the difficulties and complexities arising in this analysis and in the work of earlier investigators, it is apparent that a more detailed analysis is necessary in order to ascertain the genetic mechanism of shape and size determination in these fruits. It is a matter of common observation that in certain fruits (such as the elongate peppers) shape *changes* as growth proceeds. A study of the dimensional changes occurring during fruit development provides an obvious means of simplifying the interpretation of shape and size inheritance in the present material.

DIMENSIONAL CHANGES DURING FRUIT DEVELOPMENT

Huxley (1932) has suggested a method of studying relative growth which has already been successfully applied to the present material (Sinnott and Kaiser, 1934). Here it was shown that if length and width of ovary primordia and fruits in all stages of development, from the earliest ones observable until maturity, were plotted against each other logarithmically, the resulting curve was an essentially straight line for some varieties, while for others it was a sickle-shaped curve. Employing Huxley's formula, $y = bx^k$ where y is length and x is width, we may say that in one type (straight-development) k, the relative growth constant of length to width, remains unchanged during the growth of the fruit; since its value is nearly equal to 1, width is constantly increasing at approximately the same rate as length. In another type of pepper, an elongate one (curved-development), the developmental curve starts out just as in the previous case with the same value for k, but soon after flowering it slopes upward steeply and abruptly, indicating that length has now begun to grow at a considerably faster rate than width. As a result the elongate shape begins to emerge. Shortly before maturity, the value of k falls to 1 or less than 1,

TABLE 3

Type series of developmental fruit measurements in Line VIII, Line V and their hybrid. Asterisk indicates flowering.

VIII		V		VIII×V	
LENGTH CM.	WIDTH CM.	LENGTH CM.	WIDTH CM.	LENGTH CM.	WIDTH CM.
.06	.08	.06	.08	.06	.08
.07	.09	.08	.11	.08	.10
.08	.10	.08	.12	.09	.11
.08	.11	.10	.14	.10	.13
.10	.13	.12	.16	.12	.14
.14	.16	.14	.18	.13	.16
.17	.18	.16	.20	.14	.17
.20	.20	.18	.21	.15	.18
.22	.22	.18	.24	.18	.21
*.24	.24	*.20	.27	.21	.24
.24	.27	.24	.30	*.24	.26
.27	.22	.26	.37	.28	.32
.34	.34	.28	.32	.30	.32
.36	.32	.30	.36	.34	.33
.51	.36	.33	.42	.36	.35
.54	.36	.36	.48	.42	.40
.58	.35	.42	.54	.48	.44
.60	.39	.48	.70	.54	.45
.60	.42	.60	.75	.66	.46
.62	.38	.65	.80	.70	.40
.86	.41	.73	.88	.82	.48
1.10	.45	.85	1.05	.90	.51
1.16	.48	.90	1.20	1.05	.55
1.25	.55	1.00	1.30	1.50	.65
1.50	.58	1.12	1.50	1.50	.75
1.60	.61	1.12	1.85	2.20	1.00
1.70	.63	1.20	1.95	2.37	1.19
1.80	.65	1.27	1.70	3.03	1.16
2.50	.64	1.30	1.82	3.38	1.30
3.20	.73	1.30	2.00	3.61	1.45
3.44	.80	1.39	2.00	4.00	1.45
4.33	.86	1.60	2.30	4.05	1.65
4.90	.98			4.47	1.80
5.20	1.00			4.60	1.86
5.63	1.10				
6.07	1.09				
6.70	1.48				
7.00	1.33				
7.65	1.76				

due probably to the rapid increase in width resulting from the growth of the seeds within the ovary. Thus, in *Capsicum* fruits the stage of development at which shape genes produce their visible effect is a comparatively late one and shape differences are due to differences in the value of *k*. This determination is quite different from that in *Cucurbita* fruits where

TABLE 4

Type series of developmental fruit measurements in Line IV, Line IX and their hybrid. Asterisk indicates flowering.

IV		IX		IV×IX	
LENGTH CM.	WIDTH CM.	LENGTH CM.	WIDTH CM.	LENGTH CM.	WIDTH CM.
.06	.09	.04	.06	.08	.10
.08	.14	.05	.07	.09	.14
.09	.12	.08	.11	.10	.14
.09	.15	.09	.14	.10	.16
.10	.16	.10	.16	.12	.16
.12	.18	.12	.18	.12	.18
.13	.21	.14	.20	.15	.19
.14	.24	.15	.23	.16	.23
.18	.27	.16	.24	.18	.24
.20	.34	.17	.24	.20	.27
.21	.36	.18	.24	.22	.30
.24	.39	.18	.27	.23	.36
.28	.42	.19	.30	*.24	.30
*.30	.42	*.22	.32	.28	.40
.35	.60	.22	.36	.30	.42
.40	.70	.24	.36	.34	.49
.48	.80	.27	.41	.36	.48
.60	.85	.30	.48	.36	.54
.80	1.00	.32	.48	.40	.60
.85	1.10	.38	.58	.50	.52
.90	1.30	.42	.63	.58	.68
1.10	1.30	.50	.70	.60	.70
1.35	1.35	.55	.80	.60	.80
1.70	1.10	.66	.90	.70	.85
1.90	1.45	.70	1.10	.80	.95
2.00	1.50	.75	1.25	.90	1.15
2.10	1.40	.85	1.18	1.05	1.30
2.50	1.30	.90	1.36	1.15	1.40
2.80	1.85	.90	1.50	1.20	1.50
3.30	1.70	1.10	1.70	1.30	1.80
3.60	1.90	1.20	1.90	1.40	1.40
4.60	2.60	1.36	1.95	1.50	1.90
4.60	3.20	1.50	1.94	1.50	2.20
5.60	4.70	1.59	2.05	1.60	2.20
6.10	4.50	1.85	2.25	1.80	2.40
6.20	4.20			1.80	2.50
7.20	4.50			1.98	2.70
				2.13	2.80
				2.15	3.00
				2.30	3.05
				2.40	3.50

the various shape types are visible in the earliest primordia (due to differences in the value of b in Huxley's formula).

It is of considerable interest to examine the relative growth curves of the fruits involved in the crosses here analyzed.

The VIII×V cross. A type series of developmental measurements is given in table 3. Stages too small to measure with calipers were cut longitudinally and the median sections measured under binoculars with an ocular micrometer. The developmental curves of Line VIII, Line V, their hybrid and a selected series of F_2 plants are shown in figure 7. It will be observed that Line VIII has a sickle-shaped curve, Line V an essentially straight one, and their hybrid a sickle-shaped curve of less steep

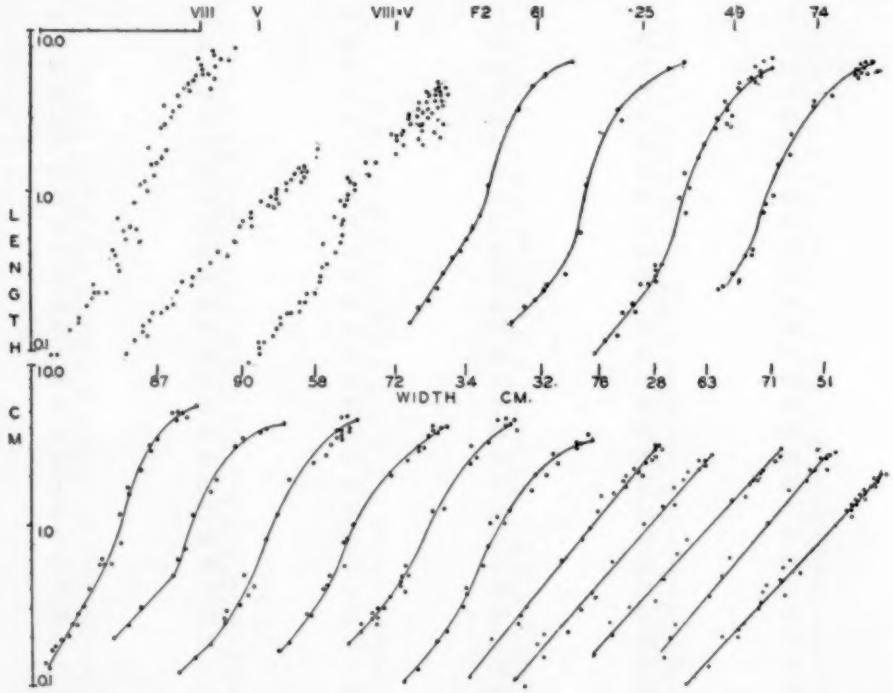

Fig. 7. Developmental curves in the VIII×V cross (above) and the IV×IX cross (opposite page). Curves of the pure lines, the F_1 hybrids and selected series of numbered F_2 plants, arranged in the order of diminishing relative length of mature fruit, are shown. The vertical lines associated with the numbers indicate the position of the 1.0 cm. (width) abscissa line for that curve.

pitch than that of Line VIII. The F_2 progeny segregates clearly into the two parental types of development. Of the forty plants thus analyzed, thirty-one were classified as curved-development types and nine as straight-development ones. In addition, four plants were analyzed but not classified because of insufficiency of measurements or marked irregularities. On the basis of this apparently monohybrid segregation it is postulated that the parental types differed in a single gene (Line VIII

carrying the dominant allelomorph) which governs the relative growth rates of the fruit dimensions in development. It should be emphasized that in the F_2 of this cross, there was *no apparent segregation in mature fruit shape*. It is thus demonstrated that shape genes may be operative in controlling relative dimensional growth rates even though the configurations of the mature fruits do not show Mendelian segregation.

The parent plants have been shown to differ in a gene controlling the

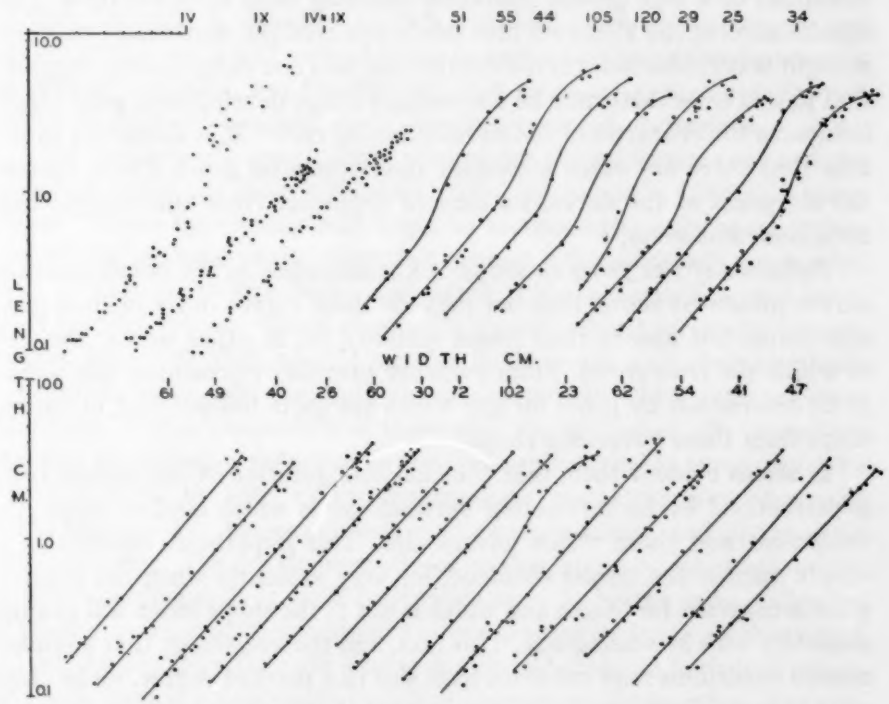

Fig. 7 (continued). See legend under fig. 7 on opposite page.

position of the mature fruit (Kaiser, 1935). On the basis of the forty F_2 plants whose phenotypes with respect to the fruit position character and the developmental curve character are known, it appears that these two genes assort independently.

The IV×IX cross. Type series of developmental measurements for Line IV, Line IX, and their hybrid are given in table 4. The developmental curves of these and a selected series of F_2 plants are shown in figure 7 (page 447). Line IV has a sickle-shaped curve somewhat different in character from that of Line VIII. Line IX has a straight one. The hybrid in this case is straight (but broken?) and the F_2 plants again segregate into

the two main development types. Of the sixty-nine plants analyzed fifteen were classified as curved, forty-eight as straight, and six as doubtful. Here too, then, is an evidently definite monofactorial segregation, but the straight type is dominant over the curved.

Among the F_2 development curves, a number were observed of a wavy, instead of continuous, character (note no. 26). It is difficult, because of an inadequate number of measurements, to say definitely whether this is fortuitous or a true genetic character resulting from recombination. The classification of the F_2 curves into thirty-five straight continuous, thirteen straight wavy, fourteen curved continuous, and one curved wavy suggests that in this cross there may be a secondary shape development gene which influences the character of the developmental curve. It is altogether probable that there are other secondary developmental genes which control the steepness of the curve, its time of departure from the straight line condition, and so on.

Influence of size genes on shape. An examination of the developmental curves presented shows that not only do these curves differ in their general shape, but also in their *length* (extent), or, in other words, the size to which the fruit grows. From evidence previously presented this seems to be determined by genes for size which are quite independent in inheritance from those governing shape.

It seems evident then, that the final configuration of the mature fruit is determined by an interaction between genes which control shape development and those which govern size. This hypothesis explains in a simple manner the results obtained, for very evidently when the relative growth constant for length and width is not 1, the shape index will change markedly with increasing size. This fact, and the knowledge that environmental conditions may influence fruit size to a marked degree, make clear why, in many cases, studies of mature fruit shapes alone result in confused and complicated situations. A knowledge of what takes place during the development of the organ seems to be the key to the solution of the main difficulties encountered in genetic studies of quantitative characters of this sort. These various shape development and size genes operate independently of each other, except where linkage occurs (which seems to be the case in the IV×IX cross), and by their assortment and recombination produce a variety of types in the F_2. These F_2 types show no clear segregation of mature fruit shape indices in the VIII×V cross but fall into two well-defined groups (the parental types) in the IV×IX cross. One might expect that in this latter cross, where a number of size factors are involved, there would also be no clear fruit shape segregation. The apparent linkage between shape and size genes here probably accounts for the results obtained.

It is clear that the genes postulated as a result of the findings of the present investigation must exert their control over fruit shape and size by governing the rates of cell division and cell enlargement and the directions in which these take place. What is the histological and developmental basis for the changes in relative growth rates and size determination which the genes control? Work is at present in progress which may throw light on the relation of cell shape and size to fruit shape and size in this material. A quantity of data obtained from measurements and counts of the ovary wall cells of fruits in various stages of development is at present available, but has not yet been thoroughly analyzed. Several points of interest, however, have already presented themselves.

The pericarp cells particularly studied are the epidermal cells and the cells just inside the inner epidermis, called by Augustin (1907) "Riesenzellen." These interesting cells begin as meristematic cells equal in size and similar in shape to the others but grow at a tremendously accelerated rate, so that in the ripe fruits they attain a size several thousand times their original volume. These giant cells are convenient for study because of their large size, their specific position in the ovary wall, their relatively constant number, and the rapid changes in growth which they undergo. It is clear, from a comparison of these with the epidermal cells that shape and size genes do not influence all the pericarp cells in the same way. The "Riesenzellen" in both curved-development and straight-development fruits are found in the ovary anlage in equal numbers, and of the same shape and size. The developmental curves (for length-width relationship) of these growing cells in both fruit types seem to be the same, following in general the curved-development pattern of elongate fruits (sickle-shaped curve). At maturity they are similar in size and shape in both fruit types, although there is considerable variation throughout the length of the fruit. The outstanding fact, however, is that in the elongate fruits, all the young "Riesenzellen" develop in this way, while in the shortened fruits, only some do so. As a result, although both types have at the start equal numbers of young "Reisenzellen," at maturity the long fruits have a larger number of mature giant cells. In the short fruits, these cells are fewer, having pushed the undeveloped "Riesenzellen" inside. These cells evidently behave differently from those studied in other material by Tenopyr (1918) and Houghtaling (1935).

DISCUSSION AND REVIEW OF PERTINENT LITERATURE

The chief contribution of the present work is its demonstration that, exclusive of the effects of environmental conditions, the ultimate configuration of the fruit of *Capsicum annuum* depends on the interaction between genes governing the relative growth rates of its dimensions and genes

controlling its absolute size. A comparison of the results obtained from the present research with the results of similar work done on other organisms suggests that the theory here proposed in explanation of the genetic determination of shape may be useful in simplifying the complexities which often arise from studies dealing with shapes of mature organs exclusively.

In several cases, specific genes controlling shape have been postulated on the basis of mature organ shape segregations. Leake (1911) obtained in cotton leaves a clear 1:2:1 F_2 segregation for "leaf-factor," a shape character. Sinnott (1927) identified two genes in *Cucurbita*, which by their interaction produce elongate, spherical, and discoid fruits. Lindstrom (1927) found genes in the tomato which determine a number of particular fruit shapes. Hutchinson (1934) described the effects of five multiple allelomorphs in cotton, which control leaf shape. The present case of the IV×IX cross parallels these simple results, but no other results reported for the fruits of *Capsicum annuum* do so. In many species, evidence from studies of mature organ characters indicates that shape as such is not inherited as a simple character. This evidence consists of the intermediate character of the F_1 and/or the continuous nature of the F_2 shape frequencies (Jones, 1911, in *Digitalis* leaves; Groth, 1915, in tomato fruits; Kakizaki, 1930, in eggplants; and Crane and Lawrence, 1933, in apples). The present case of the VIII×V cross parallels these results. But it has been shown for this cross (as well as for the preceding one) that when the fruits are studied developmentally, evidence is obtained of the activity of a single major gene which controls the shape of the organ (at a particular size) by governing the relative growth rates of its dimensions.

Except in the case of dwarf forms, specific single size genes are comparatively rare. Leake (1911) indicated that some may be present in the case of petal size in cotton flowers. Lindstrom (1932) identified several in tomato fruits through linkage studies. Green (1935) located size genes in the mouse on a particular chromosome. Castle (1929), however, failed to find any evidence of linkage of size factors in the rabbit with four known linkage groups. There is considerable disagreement among investigators as to the number and mode of operation of size factors. Rasmusson (1933) is of the opinion that "it is considered more probable that 100–200 genes are usually involved in the segregation of quantitative characters than 2–20." Others believe there are much fewer. Crane and Lawrence (1933) and more recently Lindstrom (1935) hold that size genes operate additively with partial dominance; Dale (1928) and others argue that size genes operate geometrically without dominance. From the present work, it seems clear that in the VIII×V cross a small number of size factors are involved;

in the IV×IX cross the number appears to be larger. The normalization of skewness in F_2 volume distributions when plotted logarithmically suggests that these size genes operate geometrically rather than cumulatively.

A number of investigators hold the position that dimensional characters are inherited (Dale, 1928, and Deshpande, 1933, in pepper fruits; Keeble and Pellew, 1910, and De Haan, 1927, in pea stems; Freeman, 1919, in wheat leaves; Kottur, 1923, in cotton leaves; Sirks, 1929, in broad-bean leaves; Ramiah and Parthasarathi, 1933, in rice grains). According to this idea, shape would not be a definitive hereditary character but would be the resultant of genetically determined dimensions. In almost all of these cases the genetic evidence for dimensional inheritance is at best very complicated and in many instances unconvincing. The present results and those of Sinnott mentioned earlier indicate that apparent segregations of linear dimensions in F_2 progenies are not to be regarded as evidence that genes directly regulating these dimensions exist, but rather that these segregations are the indirect results of interactions between genes controlling dimensional *relationships* during the organ's development, and genes controlling the total amount of growth.

This hypothesis finds support in the conclusions of other investigators working on a variety of materials: "Observations on F_2 bean seeds where the parents differ in size but not in shape indicate that length and breadth are probably not inherited independently of each other" (Emerson, 1910); ". . . what is inherited is (A) a defined rate of relative growth . . . , (B) a defined adult absolute size" (Ford and Huxley, 1927, on *Gammarus* limbs); "The factors determining shape are evidently those which govern growth correlations" (Sinnott and Durham, 1929, on squash fruits); "Particular dimensions are merely resultants of the interaction of these shape and volume factors" (Sinnott, 1931); "He" (Castle on rabbits) "also recognizes that body form is to some extent a function of size . . . that there are growth relations of the sort which Huxley terms heterogonic" (Wright, 1932); "The conclusion is reached that conformation is primarily the result of the interaction of growth factors . . ." (Gregory, 1933, on cattle form); "It follows therefore that size and form show a strong tendency to remain constant or to vary together, not to be modified independently of one another" (Brues, 1934, on insect size).

The importance of studying growth in development as relative growth of parts (or dimensions) rather than as growth of the whole has been emphasized here. This idea has also been stressed not only by Huxley but by D'Arcy Thompson (1917), Pearsall (1927), Robb (1929), and others. A striking demonstration of its value in evolutionary study has also been made by Hersh (1934) in his study of fossil titanotheres. Here it is shown

that changes in size result in profound changes in form when k is not equal to 1. The present paper shows the importance of this kind of treatment in genetic studies. Sinnott (1932) has previously shown that developmental studies are able to clarify complex quantitative segregations.

The developmental genes postulated in the present work apparently operate by controlling growth rates. This is in harmony with Goldschmidt's theory of the genetic determination of characters through the control of rates of reactions. It should be emphasized, however, that these developmental genes govern not merely growth velocities but the *relationships* between these velocities.

SUMMARY

1. The genetic determination of shape and size has been studied in two crosses of *Capsicum annuum* by (1) a statistical analysis of mature fruit dimensions and (2) an analysis of dimensional changes during fruit development.

2. The following facts support the theory that the hereditary control of dimensions is accomplished through the independent genetic determination of shape and of size: (1) In the cross of Line IV×Line IX, mature fruit shape index shows a clear monofactorial segregation in the F_2; in the cross of Line VIII×Line V no such segregation is observed, but the F_2 shows a complex continuous distribution of shape indices; (2) In neither cross are there simple F_2 segregations for length or width of mature fruit; (3) In the cross of Line VIII×Line V there is no significant correlation between shape and size in the F_2; in the cross of Line IV×Line IX this correlation is of the order of plus 0.5 (the longer fruits are in general larger); (4) In both crosses length is positively correlated with width in the pure types and F_1; in the F_2 this correlation is small or negative; (5) Length is almost twice as variable as width in the F_2 of both crosses; in the pure types and the F_1 these variabilities are almost equal.

3. Evidence is presented that in each cross there is a single major gene controlling the *relative* dimensional growth rates of the developing fruit. In some cases the relation between the growth rate in length and that in width is constant, in others it changes as growth proceeds.

4. Size is genetically determined by the interaction of a number of size genes, but is subject to considerable modification by environmental factors. These size genes operate geometrically, not additively.

5. The ultimate configuration of the mature fruit is genetically determined by the interaction between (1) factors governing relative dimensional growth rates and (2) factors governing the size of the fruit. In one of the crosses, these two types of genes are probably linked.

6. Developmental analyses are thus able to simplify complex genetic data obtained from studies of mature organs.

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Origin and development of the female gametophyte, endosperm and embryo in Orobanche uniflora[1]

JOSEPHINE D. CASSERA

(WITH PLATES 25–28)

INTRODUCTION

Orobanche uniflora L. (*Aphyllon uniflorum* T. & G.) is a small parasitic plant growing in moist woods on the roots of goldenrod, clover, aster, etc. It bears a few brownish ovate bracts near the base and sends up one to four erect, slender, one-flowered stalks about three to six inches high. The leaves are reduced to simple, chlorophyll-less scales with an alternate arrangement on the stem. The flowers are solitary, perfect and zygomorphic. The curved tubular five-lobed corolla is purplish or light violet to white with purplish veins. It consists of four or five united sepals and five petals united into a tube. There are four stamens in pairs inserted on the tube of the corolla and often a fifth that is reduced to a staminode. The pistil is bicarpellate with an ovary which is superior, one-celled, and has four parietal placentas. The flower is three-quarters of an inch long and externally is hairy and delicately fragrant. In general the flower structure strongly suggests that of the Scrophulariaceae.

Previous to 1917 relatively little work had been done in the morphology of the Orobanchaceae. In 1917 Scharf surmised that the Orobanchaceae were to be derived from forms which, like the majority of the Scrophulariaceae had a well-developed chalazal and micropylar haustorium. Boeshore (1920) believed that the Orobanchaceae "represents a greatly degraded offspring series or sub-family of parasitic habit that has gradually been derived from Scrophulariaceae in which slow absorption of the ovarian partitions has resulted in a one-celled state from a primitively two-celled." He proves this point by tracing the varied morphological transitional characters between Scrophulariaceae and Orobanchaceae and correlating with this a graded physiological parasitism and degradation. Carter (1928) studied the early embryology of the ovule of *Orobanche minor* and stated that the early development of the megaspore mother cell in *O. minor* was the same as Schertz (1919) described for *Scrophularia marylandica*. Glisic (1929) reported that the embryo-sac development in *O. hederae* and *O. gracilis* were of the normal type occurring in the Angiosperms but the formation of endosperm and haustoria was characteristic of Rhinantheae and Scrophulariaceae—thus confirming Scharf's and Boeshore's work. The

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Scrophulariaceae and the Orobanchaceae Glisic concluded agree so thoroughly in their endosperm characters that they could well be united; close relationship between these two families is also seen in seed development.

The purpose of this paper is to present a study of the development of the female gametophyte and endosperm formation in *O. uniflora*, making special reference to any primitiveness or specialization which may have developed as a result of its parasitic habit. During the course of this work, the writer also noted the great resemblance of the Orobanchaceae to the Scrophulariaceae.

The plants studied were collected near Milltown, New Jersey by Dr. M. A. Chrysler in the last week of May and the first week of June, 1933. *O. uniflora* was there found to be growing parasitically on *Solidago rugosa* Mill.

The ovaries of *O. uniflora* showing various stages of development were divested of the sympetalous corolla, leaving the base of it bearing the epipetalous stamens. The larger ovaries were cut transversely and longitudinally to facilitate penetration of the fixative. It was found necessary to exhaust air from the material by suction as it did not sink in the fixative. Various types of fixatives were employed. Carnoy's fluid was found to be too violent in its action and produced great shrinkage even though the material was left in the fluid only fifteen minutes. Material fixed in Carnoy's was useless for cytological study of the early stages of development of the ovule and embryo-sac, but proved successful in the fixation of the mature buds. Chrom-acetic acid and Allen's modification of Bouin's solution "PFA_3" gave results which proved to be excellent for detailed study. The buds were embedded in paraffin and serial sections of five microns and seven microns were cut and fastened serially to slides. Heidenhain's iron-alum haematoxylin counterstained with orange G in clove oil was the most suitable stain. No detail was seen without the orange G which served as a valuable background for bringing out the structure and content of the nucleus. Safranin counterstained with crystal violet was also used but details of the nucleus were not clearly seen.

OBSERVATIONS AND DISCUSSION

In *Orobanche uniflora* the microsporangiate structures have reached the mother-cell stage before the megasporangia become visible as projections from the placenta. The differentiation of the megasporangium begins with rapid cell-division in the epidermis and hypodermis which results in the even surface of the placenta becoming a mass of crowded blunt protuberances. In these the megaspore mother cell is first differentiated as an enlarging hypodermal cell rich in cytoplasm and showing a conspicuous

nucleus. The nucellus next appears as an arch of small cells at the tip of the megaspore mother cell and proceeds to surround the entire megaspore by laying down anticlinal walls. At this stage the walls of two or three outer cells of the ovule begin to bulge outward and form the integument, which is single but has a thickness of four to six cells (fig. 1). The epidermis on the side of the integument facing the nucellus then develops into a conspicuous nutritive jacket.

The megaspore mother cell next increases in size. In appearance it is an elongated cell with a large nucleus and nucleolus. In the resting stage the nucleus shows a peripheral reticulum with strands extending towards the nucleolus. On the whole the appearance of the nucleus is that of a hollow body with a non-staining nucleolus (fig. 2).

Formation of the embryo-sac

The megaspore mother cell then elongates and undergoes two consecutive divisions giving rise to a linear tetrad of megaspores (figs. 2, 3, 4). The tetrad condition was observed in every case, contrary to Miss Smith's (1901) report that the mother cell does not divide in *Aphyllon uniflorum*. After a short rest period, the chalazal megaspore, the only one to function, begins to enlarge by digesting and absorbing the other three megaspores, which gradually become smaller (fig. 4) and later disappear. They are recognized in their late stages of degeneration as shrunken dark cells or as shapeless masses on the edge of the functional megaspore (figs. 5, 7).

After a period of growth the nucleus of the functional megaspore divides into two large nuclei (fig. 6). During this division the funiculus and integument grow more rapidly on one side causing the ovule to curve around and the micropyle to lie close to the funiculus. Thus the ovule is of the anatropous type at the time the two-nucleate stage of the embryo-sac is reached. The nuclei then migrate to opposite poles of the embryo-sac and divide simultaneously, forming spindles which lie approximately at right angles to one another (fig. 7). Very few four-nucleated embryo-sacs were observed, and when observed, the resulting four nuclei were of unequal size. A large vacuole occupies the median portion of the sac. The same condition was reported by Miss Carter (1928) for *O. minor*. As the embryo-sac grows it pushes its way through the micropylar end of the nucellus and absorbs the food released by the breaking down of this layer. By the time the eight-nucleated embryo-sac is formed the nucellus has almost disappeared although traces of it are seen as dark masses or streaks along the megaspore wall of the embryo-sac. The absorption of the nucellus by the growing embryo-sac thus causes the nutritive layer (to be described later) to lie against the megaspore wall.

The mature eight-nucleated embryo sac is typical of the Angiosperms, with an egg and two synergids at the micropylar end, two prominent polar nuclei in the center and three antipodals which are in linear arrangement. The last are present at the time of fertilization and persist throughout endosperm and embryo formation (figs. 11, 13, 15, 17, 19), denoting a specialized condition. Persidsky (1926) also reported persistent antipodals for *O. cumana* and *O. ramosa* but Miss Carter (1928) found that in *O. minor* the antipodals disappear long before the time of fertilization so that the mature embryo-sac contains five nuclei instead of the usual eight. The polar nuclei lie near to each other and remain in that position until the pollen tube enters.

Fertilization

Adjacent ovules are not necessarily in the same phase of growth, for fertilized and unfertilized ones are found in the same ovary and even the fertilized ovules are in various stages. Before fertilization the male nuclei are distingushed from the embryo-sac nuclei by their smaller size and deeper stain. The passage of the male nuclei from the pollen tube to the nuclei with which they fuse is very rapid for they are seldom caught in the process. Fertilization and triple fusion occur simultaneously. The male nuclei remain in the resting condition and retain their small size and oval form even while in contact with the female nuclei.

After fertilization the embryo-sac elongates, developing a chalazal and micropylar haustorium, both of which later are filled with endosperm cells. There is variation in the different ovules as to the length which the incipient embryo-sac may attain before division of the primary endosperm nucleus takes place. In some it may grow to considerable length, while in others very little growth takes place until after the first endosperm division.

Endosperm formation

The endosperm development of Angiosperms occurs in two general methods: 1) free-nuclear divisions followed by cell-wall formation and 2) immediate cell-wall formation dividing the embryo-sac into two chambers. The second method is characteristic of Dicotyledons, particularly the saprophytes and parasites; *Cuscuta* (MacPherson, G. E., 1921) being the only parasite studied with the free nuclear type. The cause of the difference in endosperm development is not known but it is probably connected with the nutritive mechanism of the female gametophyte.

Endosperm development in *O. uniflora* is cellular from the beginning. In the first stage the fusion nucleus divides transversely in the middle of the embryo-sac and forms two chambers, a micropylar and a chalazal

endosperm chamber (figs. 10, 11). A rest period follows this division, during which time no cellular divisions occur although the surrounding cells are active. Upon renewal of nuclear activity the micropylar nucleus takes the lead by forming the micropylar haustorium as well as the endosperm proper. After a slight delay the chalazal chamber becomes binucleated and by its elongation functions as the chalazal haustorium. This does not undergo any further divisions. The micropylar development takes place along two divergent lines which will be discussed separately and referred to as type *A* and type *B*. They differ only in the early stages but soon converge and in late endosperm development both types increase in breadth in the same manner.

Type *A* is more common. The nucleus in the micropylar chamber undergoes division to form a longitudinal wall which gives rise to two elongated cells. Thus, at the end of the second stage there are present three endosperm cells (fig. 12). The nuclei of the micropylar cells become very prominent and elongate in the direction of the resting zygote (fig. 12). As a result of their division, cross-walls are formed, separating the micropylar haustorium from the endosperm proper (fig. 13). It is obvious that the micropylar haustorium arises from the endosperm and is not a modified synergid as was believed by Schlotterbeck. The third stage terminates with five endosperm cells, one of which is binucleate, acting as a chalazal haustorium. The nuclei of the elongated cells give rise to endosperm proper by their simultaneous divisions so that four (fig. 17) and later eight endosperm cells (fig. 18) result. Further development continues by the formation of transverse walls. As a consequence the fourth stage of development ends with two definite rows of cells. Another rest period now ensues, the only sign of activity being a swelling of the nutritive jacket which surrounds the gametophyte.

Although type *A* is more common, type *B* is also frequent and is usually present in the same ovary. The two types may be found side by side but are sharply distinguished from one another in the early stages of development. After the primary endosperm cell has laid down the transverse wall dividing the embryo-sac into chalazal and micropylar chambers (fig. 11), the micropylar chamber elongates somewhat and divides transversely. Consequently the gametophyte consists of a chalazal haustorial cell and two endosperm cells (fig. 14). The nuclear division of the chalazal haustorium next takes place as in type *A*. In stage three transverse walls are laid down rapidly throughout the entire length of the elongated micropylar chamber. Longitudinal walls next make their appearance and by the end of the fourth stage the two rowed condition of endosperm development is reached as in type *A*.

The later stages of endosperm formation for both types are the same, in which cell walls are formed longitudinally, transversely or obliquely, resulting in a mass of endosperm tissue. As the endosperm development proceeds, enzymatic processes set in and the nutritive jacket cells, along with several layers of cells just without, are absorbed and the material is used by the developing endosperm. The young endosperm occupies only the space outlined by the mature embryo-sac and four to five layers of cells are evident in the surrounding tissues. It is thus obvious that the endosperm tissue is being increased at the expense of the surrounding layers of cells. The later endosperm cells also press sharply into the antipodal end of the sac and the tissue bordering this region as well as the chalazal haustorium soon disintegrate and become compressed into a thin layer. As a result the antipodals come to lie in a tubular sac with the antipodals also in a degenerating state (fig. 19).

Glisic (1929) describes endosperm formation of type *A* for *O. hederae* and *O. gracilis*. He is of the opinion that this is the only type of endosperm development and doubts the results of the earlier investigators, especially Koch, Worsdell and Bernard. These workers report that the first two endosperm divisions result in cross walls that divide the embryo-sac into cells lying in definite tiers, one above the other (type *B*). Glisic then attempts to point out their error by stating that the longitudinal wall is very thin and often lies in the plane of section so is not frequently seen. According to the writer's results for *O. uniflora*, the earlier workers as well as Glisic are probably correct, for the type of development in the different species may differ, since both types occur in *O. uniflora*.

The cells of the two types of endosperm development differ, so it is not possible to mistake those of one type for the other. Two elongated cells result from the second division of endosperm development in type *A*. These cells always have nuclei which are very conspicuous and elongated. On the other hand, the second division in type *B* gives rise to two cells which are definitely box-like or rectangular in shape and contain large round nuclei. Consequently, Glisic is in error when he makes the statement that type *B* is really type *A* in which the longitudinal wall is not visible.

Haustoria

As previously mentioned, early in the development of the endosperm the chalazal chamber of the first endosperm division becomes binucleated and elongates to form the chalazal haustorium. Digestion of the nutritive cells at the antipodal end of the ovule occurs very early by the enzymatic action of the chalazal haustorium. As a result most of the antipodal walls

are broken down, leaving a loose mass of nuclei adjoining the haustorium. This organ represents a stunted haustorium which, contrary to the condition found in the Scrophulariaceae and other Sympetalae, never becomes prominent nor as highly developed as the micropylar haustorium.

The micropylar haustorium is cut off from the endosperm proper at the third division of the micropylar chamber nuclei (fig. 13). The first haustorial cells are seen as two conspicuous bulging cells with very prominent nuclei and dense cytoplasm. These two cells soon elongate and divide (figs. 17, 18) rapidly to form a long haustorium which stains deeply due to its abundant food content. Glisic (1929) reports that Koch was the first to recognize the different portions in the micropylar haustorium. The extreme part of the haustorium, which is the most striking and active, he designates the "fertile" part and the other cells making up the haustorium as the "sterile" portion. This consists of several layers (six to seven) arranged in two longitudinal rows of small plate-like cells. Toward the base this sterile portion broadens and is transformed into regular endosperm tissue.

The haustoria are prominent during the early endosperm development but become less conspicuous and show signs of degeneration; by the time the embryo is completely formed they have disappeared entirely. The chalazal haustorium is the first to degenerate and it gradually flattens until it is observed as a dark cap at the antipodal end of the endosperm (fig. 19). The cause of the degeneration is probably the pressure exerted by the aggressive endosperm tissue, although Persidsky (1929) is of the opinion that the nuclei mass together in the chalazal haustorium and by their impetus cause the rapid degeneration of the haustorium. Subsequently the cavities formed by the haustorial deterioration become narrow and no trace of them is seen in the mature seed.

The extent of the development of the haustoria appears to be related to the thickness of the integument, which in these forms is a source of nutritive supply as well as a protective mechanism. These absorbing organs have been studied particularly in the Labiatae, in certain of the Compositae and numerous Scrophulariaceae (Coulter and Chamberlain, 1903).

Nutritive Jacket

As previously mentioned (p. 457), the nutritive jacket originates from the integumental cells immediately adjacent to the nucellus. The differentiation of these cells occurs prior to reduction division in the megaspore mother cell. After fertilization the nutritive jacket which consists of one layer of cells, divides rapidly to keep pace with the growing gametophyte

(fig. 10). During early endosperm development the cells of the nutritive jacket divide mitotically so that they become binucleated (figs. 12, 13, 15, 16, 17, 18). These nutritive cells grow remarkably large and soon become vacuolated with the two nuclei lying tightly against the megaspore wall. This condition is especially conspicuous in the late endosperm formation when the nutritive jacket is resorbed and replaced by endosperm tissue.

This nutritive jacket is remarkably similar to the tapetal layer in the anther and probably serves the same function. The mitoses occurring in the jacket are all normal and regular and do not show the aberrations often seen in the tapetum. The tapetal cells are more richly supplied with food and their density probably interferes with the extension of the spindle so that abnormal mitoses occur. A similar nutritive jacket has been found to be conspicuous in *Helosis*, *Sium*, many Scrophulariaceae, *Campanula*, Stylidaceae, certain Compositae, *Lobelia*, Primulaceae (except *Leptosiphon*), *Linum*, *Forsythia*, *Amsonia*, *Menyanthes*, Polemoniaceae, *Myoporum*, *Globularia*, *Scaevola*, *Calendula*, etc. (Coulter and Chamberlain, 1903).

Embryo

During all the activity taking place in the formation of endosperm, the zygote has been in a resting condition (fig. 20). The first sign of embryo development is an elongation of the zygote (fig. 21). Nuclear division then occurs dividing the zygote into two cells, an anterior bulbous cell which is the embryo proper and the elongated suspensor (fig. 23). In no instance has the suspensor been found to consist of a series of cells. It is always unicellular and soon resorbed by the embryo (figs. 24, 25). The embryo follows the normal sequence in development but remains very rudimentary and minute.

SUMMARY

1. In *Orobanche uniflora* L. the microsporangiate structures have reached the mother cell stage before the megasporangia become visible as projections from the placenta.

2. The megaspore mother cell is differentiated as an enlarging hypodermal cell.

3. The nucellus consists of a single layer of cells.

4. The integument is single but consists of many layers of cells.

5. The integumental cells immediately adjacent to the nucellus differentiate to form the nutritive jacket. This differentiation occurs at the

time the megaspore mother cell is about to undergo reduction division.

6. The ovules are of the anatropous type.

7. The megaspore mother cell undergoes two consecutive divisions giving rise to a linear tetrad of megaspores; the chalazal one gives rise to the embryo-sac, while the other three degenerate.

8. The mature eight-nucleated embryo-sac is of the typical angiospermous type with an egg and two synergids at the micropylar end, two prominent polar nuclei in the center and three antipodals which have a linear arrangement; they are present at the time of fertilization and persist throughout endosperm development.

9. Fertilization and triple fusion occur simultaneously.

10. Endosperm development is cellular from the beginning. The fusion nucleus divides transversely and two chambers are formed, a micropylar and a chalazal one. The development of the micropylar part takes place along two divergent lines. These differ only in the early stages but soon converge and in late endosperm development both types increase in breadth in the same manner. The chalazal chamber becomes binucleated, elongates and functions as a chalazal haustorium in both types.

11. A well-developed micropylar haustorium and a stunted chalazal haustorium are active during endosperm development but degenerate and entirely disappear during late embryo development.

12. A very conspicuous and highly specialized nutritive jacket surrounds the gametophyte; the endosperm tissue ultimately resorbs this layer.

13. The embryo follows the normal sequence in development but remains very minute and rudimentary. The suspensor is always unicellular and is soon resorbed by the embryo.

14. The nutritive mechanism in *O. uniflora* is very complicated and efficient, nutritive substances being derived from the nucellus by the growing embryo-sac; from the nutritive jacket by the embryo and newly formed endosperm cells; and from the integument by the encroachment of the haustoria.

The writer wishes to express her appreciation to Dr. M. A. Chrysler, under whose direction this work was carried out, for valuable suggestions, helpful advice and criticism.

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Explanation of Plates

Drawings were made with an Abbé camera lucida at table level. Zeiss 5×, 10× and 15×oculars and a Spencer 1.8 mm. oil immersion objective were used. Abbreviations used in the plates are: CEC, chalazal endosperm chamber; CH, chalazal haustorium; E, endosperm; EM, embryo; LA, linear antipodals; MEC, micropylar endosperm chamber; MH, micropylar haustorium; NJ, nutritive jacket; S, suspensor, Z, zygote.

Plate 25

All drawings are magnified ×1156.

Fig. 1. Young ovule showing the megaspore mother cell, single layer of nucellus and the integument still in its formative stage.

Fig. 2. Megaspore mother cell.

Fig. 3. Two-nucleated megaspore mother cell.

Fig. 4. Linear tetrad of megaspores with the chalazal one enlarging at the expense of the other three.

Fig. 5. Functional megaspore; the other three in a degenerated condition.

Fig. 6. Two-nucleated embryo-sac with the three outermost megaspores still present.

Fig. 7. Two-nucleated embryo-sac in process of division.

Fig. 8. Four-nucleated embryo-sac.

Fig. 9. Mature embryo-sac.

Plate 26

All drawings are magnified ×528.

Fig. 10. First division (transverse) of primary endosperm nucleus. Nutritive jacket surrounds the megaspore wall.

Fig. 11. Micropylar and chalazal endosperm chambers. Antipodals in linear arrangement at antipodal end of embryo-sac. Zygote in resting condition.

Fig. 12. Second division (longitudinal as in type *A*) of endosperm nucleus resulting in three endosperm cells.

Fig. 13. Third division (transverse as in type *A*) in endosperm development resulting in five endosperm cells. Nutritive jacket conspicuous and binucleated. Antipodals and zygote also seen.

Fig. 14. Second division (transverse as in type *B*) occurs in micropylar chamber, resulting in three endosperm cells, one of which constitutes the chalazal haustorium.

Fig. 15. Simultaneous divisions (transverse as in type *B*) occurring in micropylar chamber. Chalazal haustorium is binucleated.

Plate 27

All drawings are magnified ×528.

Fig. 16. Endosperm formation accomplished by transverse walls (type *B*). Binucleated condition of nutritive jacket clearly seen.

Fig. 17. Nuclei in act of division to give four-celled endosperm stage of type *A*. Zygote and antipodals also present.

Fig. 18. Nuclear divisions which will result in eight-celled endosperm stage of type *A*.

Fig. 19. Complete endosperm formation. Chalazal haustorium almost gone; micropylar haustorium also in degenerating condition. Embryo is embedded in endosperm tissue. No trace of nutritive jacket seen.

Plate 28

All drawings are magnified ×750.

Fig. 20. Resting zygote.

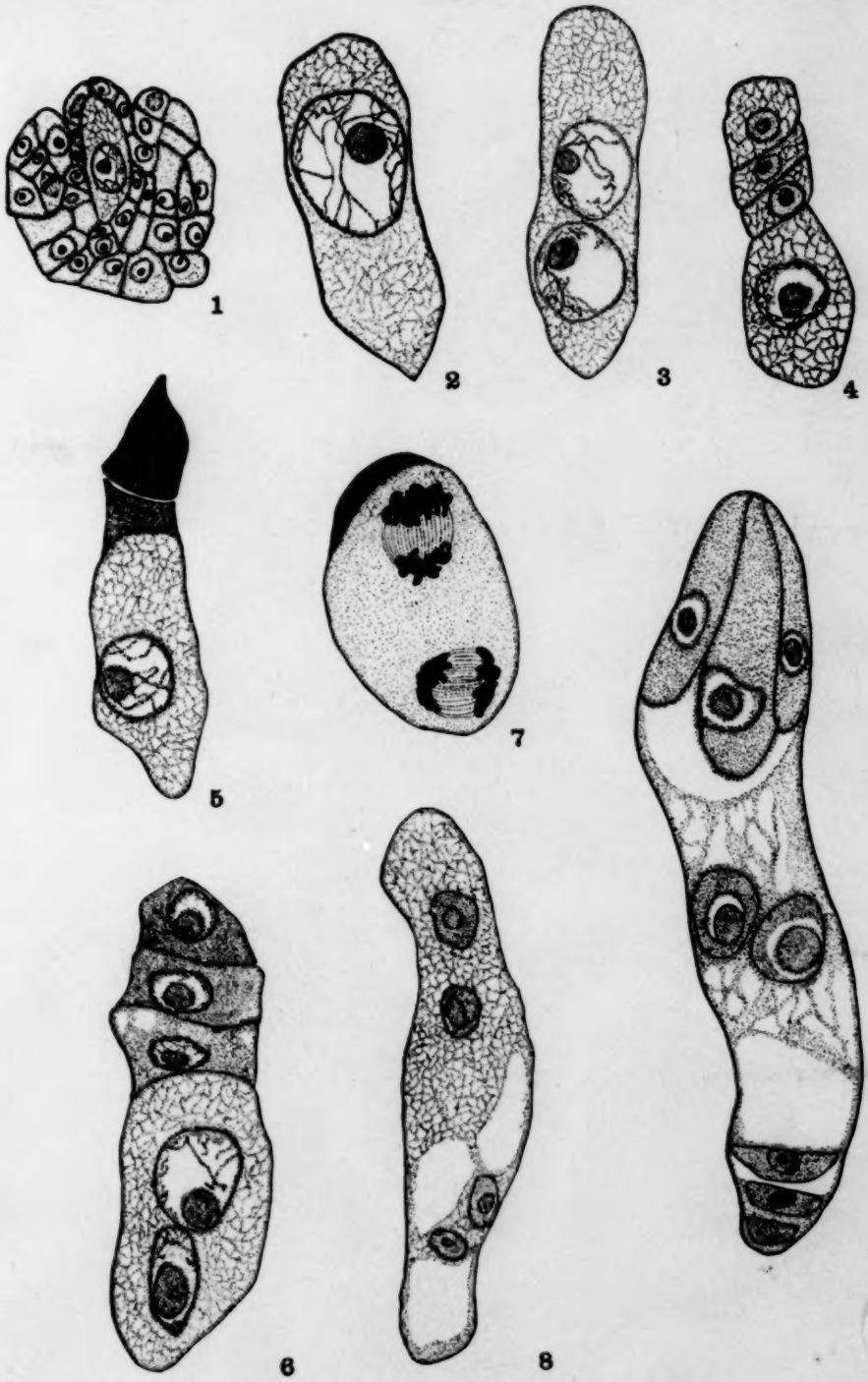
Fig. 21. Zygote in act of elongation prior to first division.

Fig. 2. Spindle of first zygote division.

Fig. 23. First zygote division (transverse) resulting in embryo and elongated suspensor.

Fig. 24. Longitudinal division of embryo and resorption of suspensor by embryo.

Fig. 25. Young embryo.



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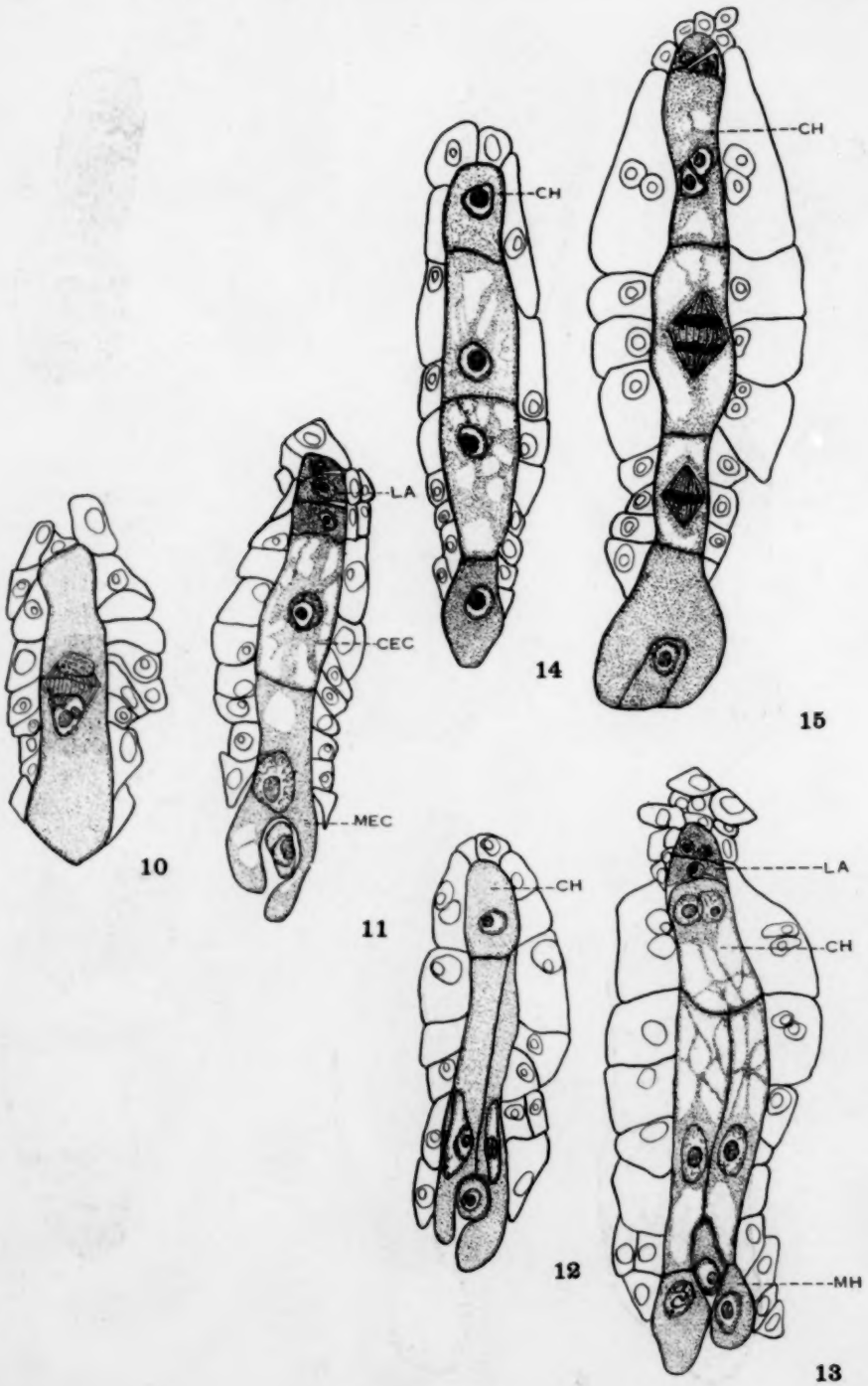
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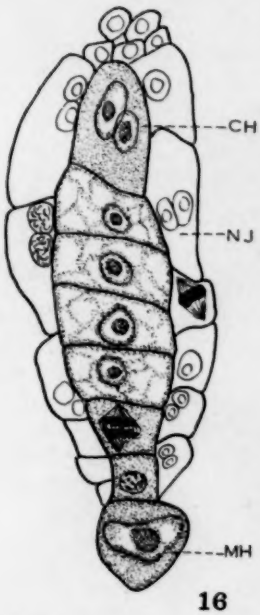

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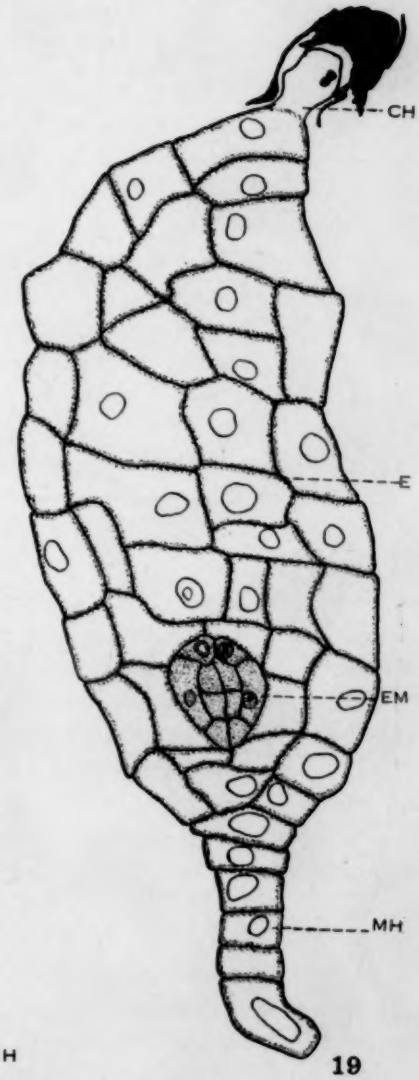

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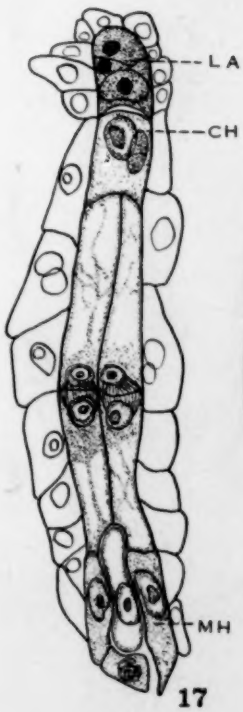

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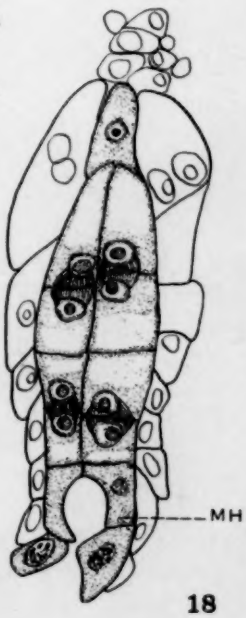

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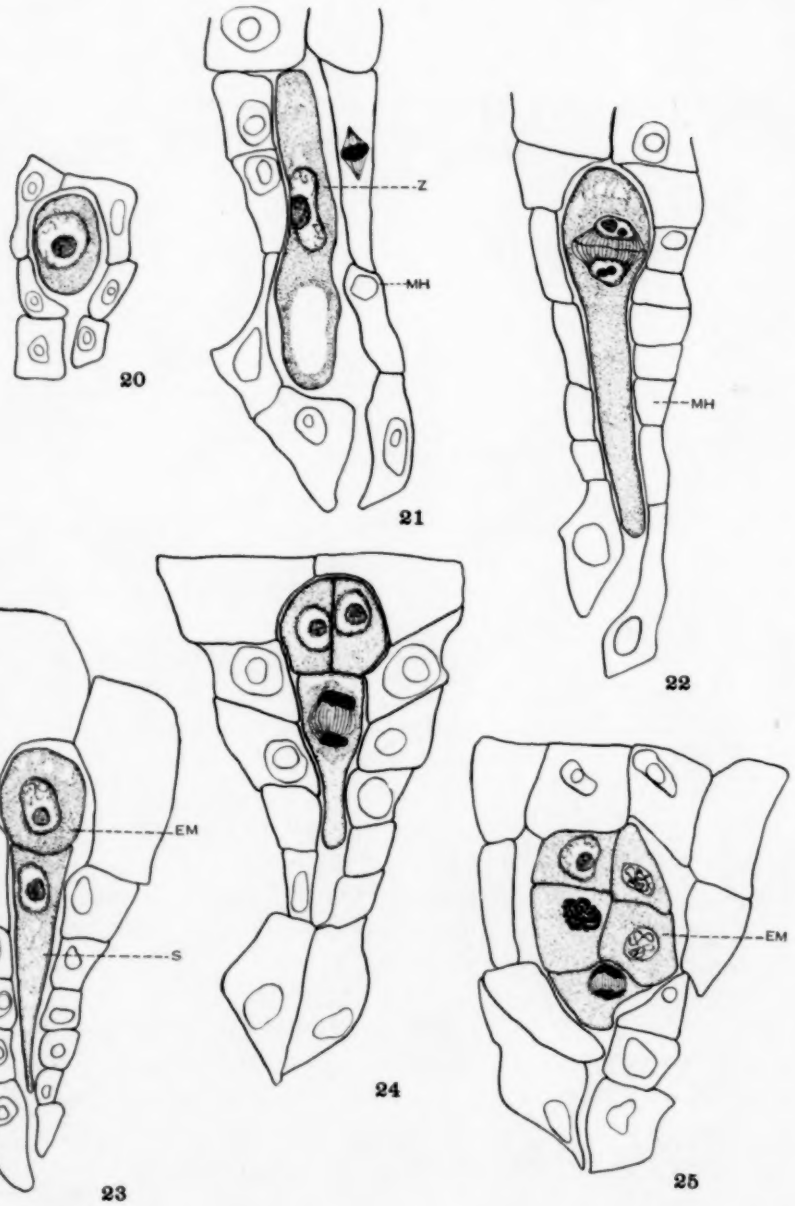

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The floral anatomy and probable affinities of the genus Grisebachiella

ROBERT E. WOODSON, JR.

(WITH TWO TEXT-FIGURES)

The vast plateau of Patagonia, extending from the Atlantic coastal plain westward to the Andes, and roughly comprising the Argentine territories of La Pampa, Neuquen, Rio Negro, Chubut, and Santa Cruz, is one of the botanical enigmas of South America. Predominantly somewhat barren and with but relatively scant and monotonous vegetation, the gradually uplifting terrain is traversed by several streams of considerable size draining from the foothills of the western mountains. Small seasonal lakes are found almost throughout the region; arid hills disrupt the nearly flat or rolling topography at monotonous intervals. This country is Argentina's "wild west"; and like most grazing countries, it is of little attraction to the botanical collector to whom it is consequently little known. Among the foothills of the Andes to the west, however, Patagonia is of an entirely different aspect. The boundary between Chile and Argentina is strewed with innumerable lakes of great charm and a luxuriant vegetation of much interest exists.

Our knowledge of the plants of Patagonia is largely dependent upon the collections of P. G. Lorentz and G. Niederlein during the past century. During the course of a collecting expedition to the upper valley of the Rio Negro in June 1879, the latter collected at two localities ("en los declives de las barrancas en las orillas del Rio Neuquen; entre el Rio Curruleubu y el Rio Colorado.") a peculiar flowering plant which was subsequently described by Dr. Lorentz (1880) as a new genus and species which he named *Grisebachiella Hieronymi*, the specific epithet commemorating Dr. G. Hieronymus in whose company the author had spent some time in the botanical exploration of Argentina.

Grisebachiella Hieronymi is a low undershrub said by the collector of the type specimen to attain a height of two to three decimeters, the stems woody, 0.5–0.75 cm. in diameter at the base, the surface with a smooth, pale yellow periderm bearing relatively distant, horizontal lenticels when fully mature. The phyllotaxy is decussate and the branches are opposite. The leaves are relatively inconspicuous, 1.0–1.5 cm. long, shortly petiolate, and ovate, the apex acute to obtuse, minutely mucronulate, the base rounded to truncate. The texture of the leaves is subcoriaceous, the color pale green, somewhat glaucous, and the surface glabrous; the margin is entire. No glands or other special emergences are borne upon the midrib or

petiole. The inflorescence is lateral and uniflorous. About midway upon the stalk of the flower a poorly developed protuberance is found, suggestive of a vestigial floral member. This "stalk" varies from 0.15 to 0.2 cm. in length and is strongly reflexed at maturity. The five-parted calyx is finely papillate without, like the axis of the inflorescence, and the lobes are broadly oblong, averaging about 0.2 cm. in length. At the base of the calyx within are found very inconspicuous groups of glandular emergences or "squamellae" alternating with the lobes. The corolla is rotate and five-parted, the lobes are obliquely oblong, about 0.15 cm. long, and the extremely short tube somewhat less than 0.05 cm. in diameter at the base. Like the calyx, the corolla is minutely papillate without. The very minute anthers are attached to the base of the corolla-tube and are approximately 0.05 cm. long. The pistil consists of two carpels united at their apices by a short, common style surmounted by a capitate, obscurely bilobed stigma about equal to the bulk of the ovary. The anthers are closely connate and appressed to the stigma.

Although none of the available specimens of Niederlein's original collections show any trace of fruit or fruiting pedicels, Lorentz (1880) referred very vaguely to such in his description ("Fructus fragmentum solum modo obtinuimus;" "fructus completus et semina deficiunt."), and in a plate published the year following (1881) a figure is introduced purporting to illustrate the fragmentary fruit, which is unrecognizable as such, evidently consisting of a loose and detached mass of tissue from a larger object. The very dubious status of our information concerning the fruit of the genus will become increasingly evident from structural details of the gynoecium to follow.

Dissection rendered difficult by the small size, and interpretation uncertain by the scantiness of the material available for his study, Lorentz assigned the new monotypic genus to the family Apocynaceae, subfamily Echitoideae where it has since remained. In 1895 Dr. K. Schumann (1895) reviewed the Apocynaceae for Engler & Prantl's "Die natürlichen Pflanzenfamilien," but was so baffled by *Grisebachiella* that he merely stated that he had been unable to investigate it ("Die Gattung *Grisebachiella* Lorentz . . . habe ich nicht untersuchen können."), a peculiar situation, since the Berlin herbarium is the repository of the type specimen.

In 1897 the second, and apparently the most recent, collection of the species was made by P. Dusen: "ad Rio Limay, prope Lago Nahuelhuapi," one of the picturesque lakes of the Chilean-Argentinan border. Unfortunately fruit was again unavailable for this collection, which was made nearly a month later than that of Niederlein.

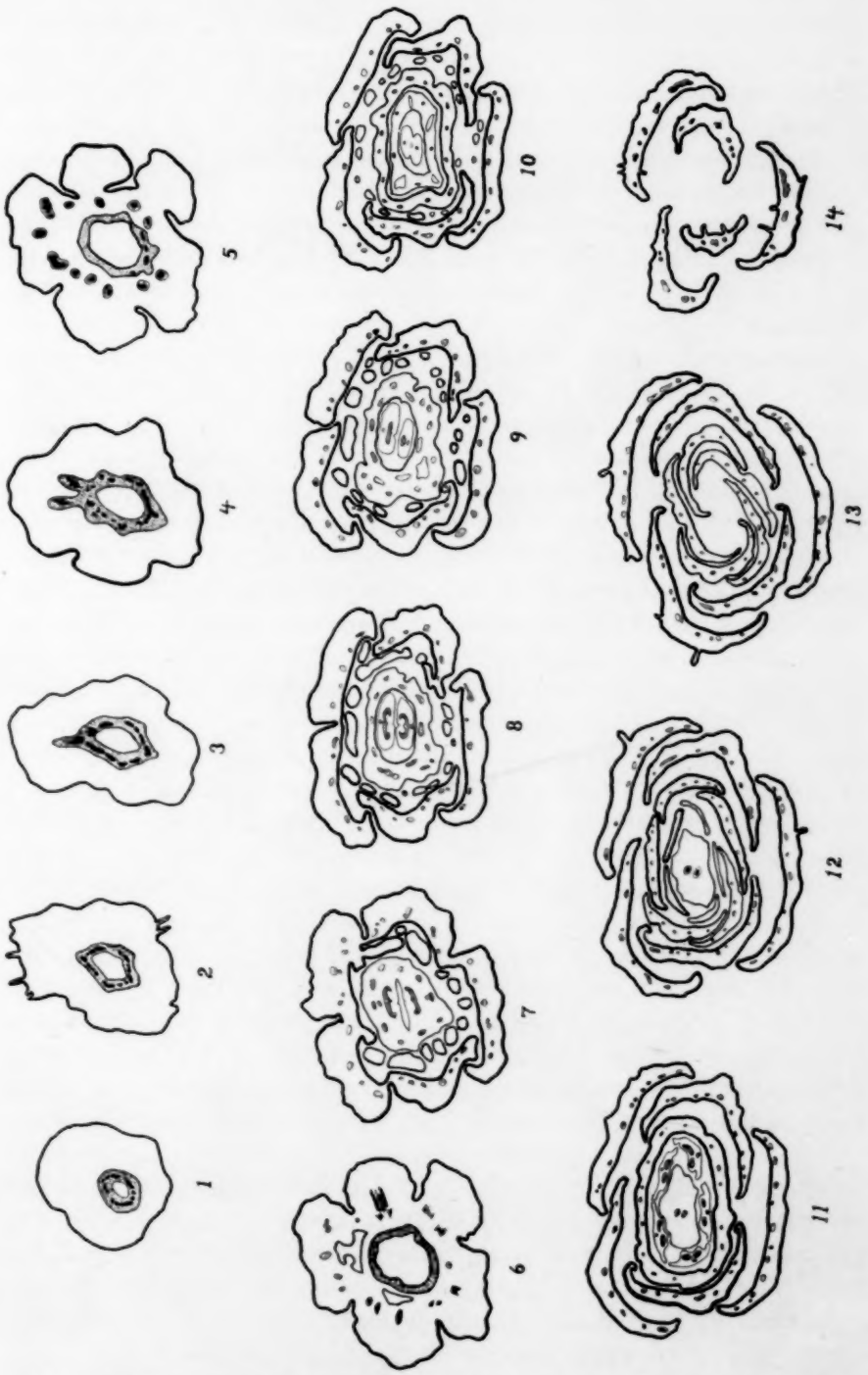

Fig. 1. Transverse sections of the pedicel and flower of *Grisebachiella Hieronymi* Lorentz. Xylem shaded, phloem stippled, anther and ovary cavities cross-hatched. Explanation in the text.

During the course of a survey of the American genera of the subfamily Echitoideae of Apocynaceae the present writer was faced with the necessity of a greater understanding of the morphology of the obscure *Grisebachiella Hieronymi*, and made a special effort to obtain material for study. No specimens were found in the herbaria of the United States, and upon visiting and inspecting most of the larger collections of Europe only the two specimens of Niederlein and that of Dusen were found in the botanical museum at Berlin-Dahlem. Inquiry of the Museo Argentino de Ciencias Naturales brought the report that the genus is unrepresented in the herbarium of that institution.

The three herbarium specimens available were graciously lent upon request by Dr. L. Diels, director of the Botanischer Garten und Museum, Berlin-Dahlem, for convenient morphological study at the Missouri Botanical Garden. From each of the specimens a single well-formed floral bud was removed. Care was taken to select the buds at the same relative stage of development, e.g. at about anthesis. They were then soaked in a stender dish of water placed in a paraffin oven at about 50°C. for a period of four days. Various methods have been recommended by the relatively few morphologists who have used herbarium specimens for the study of floral anatomy, including such softening agents as dilute solutions of caustic potash and ammonia water. These had been tried previously at various times with rather dubious success by this writer, who consequently decided to try the substitution of the proprietary reagent "Diaphanol" after the soaking in warm water. After treatment with that reagent for three days, the material was washed in 70% ethyl alcohol and passed through the usual series of alcohol and xylol to paraffin. The material sectioned well at 10μ and the serial, transverse sections were stained in crystal violet and erythrosin.

The stele of the pedicel of *Grisebachiella Hieronymi* is bicollateral, as in all known Apocynaceae and Asclepiadaceae, and consists of a number of protoxylem strands embedded in a cylinder of protophloem parenchyma (fig. 1, diag. 1). As the stele gradually approaches the receptacle it increases somewhat in volume and diameter, assuming a roughly pentagonal outline in transverse section (fig. 1, diag. 2). The central pith has increased in volume, and it is also seen that the amount of protoxylem strands have noticeably multiplied. The increase of xylem is found to continue in the two succeeding sections illustrated, during the first of which each of the five angles of the pentagonal stele prepare to supply the calyx-lobes with a single trace (fig. 1, diag. 3). In the second section (fig. 1, diag. 4), the five prominent angles gradually become somewhat greater in number, evidently approximating the traces of all ten perianth members.

In figure 1, diag. 5, the five traces have been freed to the calyx-lobes, the bases of which are becoming cleft from the non-vascular tissues of the receptacle. These traces give rise to two or four laterals shortly after leaving the stele. It will be noticed in diagrams 5–6 of figure 1 that the withdrawal of the calyx traces removes all xylem from the receptacular stele which remains. Whether the state of the stele should now be described as provascular, or as composed entirely of protophloem parenchyma is somewhat problematical. In diagram 6 it is seen that the stele assumes a roughly circular outline at about the time that the calyx-tube becomes cleft from the receptacle proper. At even the earliest stages of this cleaving, however, the origin of the squamellae is found to be marginal with respect to the concrescent margins of the calyx-lobes.

Figure 1, diag. 7 discloses the further splitting of lateral veins in the calyx. In these, however, the last trace of xylem has disappeared. The calycine squamellae have increased in number, and are assuming a circular position about the base of the corolla-tube. The corolla-tube is found to be adnate to the base of the bicarpellary ovary, the two cavities and inconspicuous axile placentae of which are seen separated by a conspicuous cavity. Ten delignified bundles occupying the corolline tissue are interpreted as the bundles of the five corolla-lobes and the five epipetalous stamens, although there appears little with which to actually distinguish them, save by their positions relative to the calyx-lobes. From two bundles at diametrically opposite sides of the circle of bundles, two smaller, delignified bundles are freed, which are immediately recognizable as the median traces of the two carpels. It is discovered that a curious situation of adnation is presented here, in which the median trace of one carpel (the upper in fig. 1, diag. 7) is adnate to a staminal trace, while that of the other is adnate to a corolline trace.

In figure 1, diag. 8, the carpels have become freed from the corolla-tube. The median traces have not formed laterals, however, and it is consequently not surprising to find that no ovules have been formed upon the marginal placentae. The corolla-tube is becoming roughly pentagonal in this section, the corolline traces migrating to the angles, and there giving rise to two lateral veins each. Diagram 9 of the same figure shows two cavities formed within the thickened angles of the corolla-tube. It is by means of the continued growth of five such cavities that the staminal filaments are finally freed from the corolla-tube. It should be noticed in the succeeding diagram that although the union is brief, a staminal column must doubtless be interpreted. In this diagram also, the first indications of the segmentation of the individual, staminal filaments is apparent as a series of radial furrows. In figure 1, diag. 11 a section is illustrated through

the anthers and stigma. The anthers are found to contain but two rather small cavities. Within the cavities were found a number of small pollen grains without an exine. The fact of their maturity, however, was indicated by their maintenance in gradually disintegrating tetrad formation. The cells of the herbarium material had been sufficiently preserved in spite of desiccation to show contents, and the general tissue systems were conspicuous. It is of great importance to emphasize at this point that the remains of the tapetal layer, as a parietal layer of disorganizing, *isolated* cells was obvious. The median traces of the carpels have continued unbroken to the stigma, while the dorsal and lateral traces of the corolla-tube have broken up into a larger number of equal veins.

Diagram 12 of figure 1 illustrates a section through the free tips of calyx- and corolla-lobes and anthers. A surprising phenomenon, however, is seen in the increased size of the carpellary traces of the stigma, which have suddenly acquired several strands of protoxylem for either. It is difficult to assign a causal function for this sudden return of lignification. No evidence of glandular cells could be found upon the stigmata. Diagrams 13–14 of figure 1 merely complete the anatomical representation of the flower.

Fig. 2. Transverse sections in the region of the bracteate node, inflorescence of *Grisebachiella Hieronymi* Lorentz. Xylem shaded, phloem stippled. Explanation in the text.

Figure 2 represents the anatomy of the peculiar protuberance previously mentioned as occurring midway upon the "stalk" of the solitary, lateral inflorescence. The "protuberance" is found to be a minute appendage provided by a single leaf-trace which is lignified. Upon the departure of this tiny bract, two glandular, marginal emergences are formed at the base, which are evidently the homologues of the calycine squamellae, the significance of which will be treated in a subsequent paper in preparation.

DISCUSSION

This writer has been engaged for several years in the taxonomy and floral anatomy of Apocynaceae during which a majority of the generic representation of the family has been studied critically. Recourse has been had from time to time to the neighboring Asclepiadaceae as a necessary correlation. From the results of such anatomical studies, five important structural features indicate the genus *Grisebachiella* as more properly relegated to Asclepiadaceae than to Apocynaceae. Of these, the massive capitate stigmatic head with obscure, apical protrusions is a similarity easy to observe from a gross dissection. Scarcely capable of observations save from anatomical preparations are the union of the staminal filaments where they are attached to the corolla, and the bilocular condition of the anthers themselves, both characters observed in many Asclepiadaceae, and in no member of Apocynaceae known to the writer. The pollen grains, which were just breaking from the tetrads, show no tendency toward the formation of an exine and are therefore in the category of glutinous pollen, characteristic of Asclepiadaceae of the subfamily Cynanchoideae. Another technical anatomical character is the adnation of the ovary to the base of the corolla-tube. In all Apocynaceae, apparently, the ovary is subinferior, the cavities sunk in the tissues of the receptacle before the cleavage of the calyx-lobes. In this family the base of the corolla is evidently never adnate to the ovary above the receptacle.

In spite of the undeniably poor understanding of a genus possible on the basis of only three herbarium specimens, one is led to suspect that there is good biological reason for the absence of fruit. It has been found that the median trace of the carpel of *Grisebachiella* does not give rise to lateral, ovuliferous traces. The ovules themselves are lacking. Lorentz, and others who examined the specimens previously, were led to exclude the possibility of an affinity with Asclepiadaceae because of the absence of pollinia. The reason for this absence is evidently disclosed from a study of microtome sections as the result largely of the complete disorganization of the tapetal cells, the dead walls of which compose the containing membranes of the pollinia of other Asclepiadaceae (Corry, 1883). The same deficiency has evidently been responsible for the non-development of the translator mechanism. Since the pollen of Asclepiadaceae is dependent upon the mechanism of the pollinia in entomophily, the default of such leaves the pollen grains, if potent, literally imprisoned within the anthers with no means of dispersal.

While it is doubtless treading on very thin ice to dwell upon the evidence of three desiccated specimens, particularly with regard to the

peculiar tendencies which appear to be manifest in them, the fact of the rarity of the plants remains. Additional observations of the plants in the field are greatly to be desired.

SUMMARY

1. The history, morphology, and anatomy of *Grisebachiella Hieronymi* Lorentz are discussed.

2. The genus is interpreted as Asclepiadaceous rather than Apocynaceous.

3. The solitary, lateral flowers are apparently derived from a pluriflorous inflorescence.

4. An explanation, from anatomical observations of herbarium specimens, is suggested for the circumscribed distribution and insufficiently authenticated sterility of the genus.

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Recent changes in the composition of a local flora

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In view of the interest now attaching to plant distribution, and to changes taking place in local distribution through clearing of woods, grazing, etc., it has seemed worth while to study certain early lists of plants of eastern New York State, to discover, if possible, the relations of the present local floras to those of a century ago. The following paper is an attempt to do this for the vicinity of Kinderhook, Columbia County, New York, by a study of two lists of plants published in the 52nd and 53rd Annual Reports of the Regents of the University of the State of New York (1839 and 1840), by W. V. S. Woodworth, Principal of the Ladies' Department in Kinderhook Academy.

The first list, entitled "A Catalogue of Indigenous Plants Found Growing in the Vicinity of Kinderhook Academy, and Analyzed by the Botanic Class in this Institution, during the Summer of 1838," bears the final note that "many plants had escaped notice until the most favorable season for examining them had past." The later list has essentially the same title, with the note that "the above catalogue embraces most of the plants which are found in this vicinity, and, with few exceptions, would show the botanic features of Columbia County." The second list contains about one and one-half times as many names as the first, but many of the same plants are given in both, and the two catalogues may be considered together. A total of 247 species is recorded; these are merely in the form of lists, with no data as to the plants themselves, their habitats, or the authors of the binomials. No indication is given as to methods of identification, but it seems probable that use was made of Eaton's "Manual of Botany" (7th Ed. Albany 1836), as this work was in use in a majority of the Academies of the state at the time, and the nomenclature of Woodworth's lists follows it closely.

In the following discussion, nomenclature will follow the seventh edition of Gray's Manual, with some exceptions, as published in House's "Annotated List." No attempt will be made to give the names as published by Woodworth except in the case of critical species, or where there is some doubt as to the meaning of a name; at such times the names as originally published will be given in parentheses.

The writer spent most of the summer of 1933 in the field, in and around Kinderhook, and all the species mentioned below, unless otherwise noted, are represented by herbarium specimens either in the New York State herbarium, at Albany, or in the herbarium of the University of Pennsylvania, at Philadelphia, or in both.

The village of Kinderhook is situated in the Hudson Valley, in the northwestern part of Columbia County, about five miles from the Hudson River. Its altitude is about 250 feet above sea-level. It lies on a post-glacial sand plain, which, outside the village, is now given over chiefly to apple orchards. South and east of the village runs the Kinderhook Creek, which is of some size, and drains a large part of the county; beyond the creek lies a rather hilly country with dry shaly soil. All the nearby woodland is second-growth, with no large undisturbed areas. Practically all the soil in the vicinity of Kinderhook is acid in reaction, except some of the alluvial land and swamps.

By going over the lists of Woodworth, it may be seen that about seven-eights of the species are common (or locally so) near Kinderhook at the present time. These may be placed for convenience in the following nine groups, of which the first eight represent roughly the associations in which the plants are found growing at the present day:

I. PLANTS TYPICAL OF LOW OR MOIST WOODS

Arisaema triphyllum (L.) Schott.
Uvularia grandiflora Sm.
Uvularia perfoliata L.
Oakesia sessilifolia (L.) Wats.
Erythronium americanum Ker.
Smilacina racemosa (L.) Desf.
Polygonatum pubescens (Willd.) Pursh (Convallaria biflora)
Medeola virginiana L.
Trillium erectum L.
Hypoxis hirsuta (L.) Coville
Cypripedium pubescens Willd. (Cypripedium pubescens)
Habenaria psycodes (L.) Sw. (Habernaria fimbriata)
Populus deltoides Marsh. (Populus angulata)
Juglans cinerea L.
Carya cordiformis (Wang.) K. Koch (Carya amara)
Corylus americana Walt.
Ulmus americana L.
Ulmus fulva Michx.
Polygonum virginianum L.
Claytonia virginica L.
Ranunculus abortivus L.
Ranunculus recurvatus Poir. (Ranunculus hirsutus)
Thalictrum dioicum L.
Anemonella thalictroides (L.) Spach.
Anemone quinquefolia L.
Coptis trifolia (L.) Salisb.

Cimicifuga racemosa (L.) Nutt.
Actaea alba (L.) Mill.
Actaea rubra (Ait.) Willd. (Actea americana)
Podophyllum peltatum L.
Sanguinaria canadensis L.
Dentaria diphylla Michx.
Ribes floridum L'Her.
Geranium maculatum L.
Zanthoxylum americanum Mill.
Acer rubrum L.
Impatiens biflora Walt.
Impatiens pallida Nutt.
Viola pubescens Ait.
Circaea lutetiana L.
Aralia racemosa L.
Sanicula marilandica L.
Nyssa sylvatica Marsh. (Nyssa multiflora)
Collinsonia canadensis L.
Pedicularis canadensis L.
Galium tinctorium L.
Solidago flexicaulis L.
Solidago altissima L. (Solidago canadensis)
Solidago canadensis may occur, but S. altissima is the common species here.

II. PLANTS TYPICAL OF SWAMPY OR BOGGY LAND OR MUCK

Larix laricina (DuRoi) Koch (Pinus pendula)
Typha latifolia L. (Typhilla latifolia)
Sagittaria latifolia Willd. var. (Sagittaria sagittifolia)
Calla palustris L.
Symplocarpus foetidus (L.) Nutt.
Acorus Calamus L.
Juncus effusus L. var. solutus Fern. & Wieg. "The common form of the species especially southward in the state—" (House).
Iris versicolor L.
Spiranthes cernua (L.) Richard.
Alnus rugosa (DuRoi) Spreng. (Alnus serulata)
Polygonum arifolium L.
Polygonum sagittatum L.
Polygonum punctatum Ell.
Caltha palustris L.
Viola cucullata Ait. "In wet places . . . common throughout the state" (House).
Cicuta bulbifera L.

Cicuta maculata L.
Cornus stolonifera Michx. (Cornus alba)
Rhododendron viscosum (L.) Torr.
Kalmia angustifolia L.
Kalmia polifolia Wang. (Kalmia glaucus)
Vaccinium corymbosum L.
Steironema ciliatum (L.) Raf.
Fraxinus nigra Marsh.
Menyanthes trifoliata L.
Scutellaria galericulata L. (Scutellaria cordifolia)
Chelone glabra L.
Galium trifidum L.
Cephalanthus occidentalis L.
Lobelia Kalmii L.
Eupatorium perfoliatum L.

III. PLANTS TYPICAL OF MEADOWS, USUALLY MOIST ONES

Lilium canadense L.
Smilacina stellata (L.) Desf.
Polygonatum commutatum (R. & S.) Dietr.
Sisyrinchium gramineum Curtis. (Sisyrinchium anceps)
Anemone canadensis L.
Penthorum sedoides L.
Saxifraga pennsylvanica L.
Geum rivale L.
Spiraea latifolia Borkh. (Spirea salicifolia)
Spiraea tomentosa L.
Veronica virginica L.

IV. PLANTS GROWING IN LAKES AND PONDS

Pontederia cordata L.
Castalia odorata (Ait.) W. & W.
Nymphaea advena Ait.

V. PLANTS OF STREAM BANKS

Ranunculus repens L.
Platanus occidentalis L.
Acer saccharinum L. (Acer dasycarpum)
Teucrium canadense L.
Stachys tenuifolia Willd. var. aspera (Michx.) Fern.
Lycopus americanus Muhl. (Lycopus europeus)
Mimulus ringens L.
Veronica americana Schwein. (Veronica anagallis)
Lobelia cardinalis L.

VI. PLANTS OF OPEN WOODS AND THICKETS

Smilax herbacea L.
Populus tremuloides Michx.
Polygonum scandens L.
Phytolacca americana L.
Clematis virginiana L.
Fragaria virginiana Duchesne
Geum virginianum L.
Rosa carolina L. (Rosa parviflora) "Frequent or common, outside the higher Adirondacks, across the state" (House).
Rubus idaeus L. var. aculeatissimus (Mey.) R. & T. (Rubus strigosus)
Rubus occidentalis L.
Rubus sp.? No doubt a high-bush Blackberry. (Rubus villosus)
Prunus virginiana L.
Epilobium angustifolium L.
Vaccinium vacillans Kalm.? (Vaccinium virgatum)
Vaccinium pennsylvanicum Lam.? (Vaccinium tenellum)
Cuscuta Gronovii Willd. (Cuscuta americana)
Verbena hastata L.
Verbena urticaefolia L.
Diervilla Lonicera Mill.
Sambucus canadensis L.

VII. PLANTS OF DRY WOODS

Pinus rigida Mill.
Pinus resinosa Ait.
Pinus Strobus L.
Tsuga canadensis (L.) Carr. (Pinus canadensis)
Maianthemum canadense Desf.
Epipactis pubescens (Willd.) A. A. Eaton.
Carya ovata (Mill.) K. Koch (Carya alba)
Ostrya virginiana (Mill.) K. Koch
Betula lenta L.
Betula lutea Michx. f.
Fagus grandifolia Ehrh.
Castanea dentata (Marsh.) Borkh.
Quercus alba L.
Quercus velutina Lam.
Hepatica americana (DC.) Ker.
Anemone virginiana L.
Aquilegia canadensis L.
Sassafras variifolium (Salisb.) Ktze.
Saxifraga virginiensis Michx.

Mitella diphylla L.
Hamamelis virginiana L.
Amelanchier canadensis (L.) Medic. (Aronia botryapium)
Prunus serotina Ehrh.
Acer pennsylvanicum L.
Acer saccharum Marsh. (Acer saccharinum)
Tilia americana L.
Aralia nudicaulis L.
Osmorhiza longistylis (Torr.) DC. (Uraspermum claytonia)
"Frequent or common northward across the state." (House).
Cornus canadensis L.
Cornus florida L.
Chimaphila umbellata (L.) Nutt.
Pyrola americana Sweet.
Monotropa uniflora L.
Rhododendron nudiflorum (L.) Torr.
Gaultheria procumbens L.
Gaylussacia baccata(Wang.) Koch (Vaccinium resinosum)
Lysimachia quadrifolia L.
Trientalis americana (Pers.) Pursh
Fraxinus americana L.
Asclepias quadrifolia Jacq.
Hedeoma pulegioides (L.) Pers.
Aureolaria virginica (L.) Pennell (Gerardia flava)
Veronica officinalis L.
Galium lanceolatum Torr.
Mitchella repens L.
Sambucus racemosa L.

VIII. PLANTS OF DRY FIELDS

Pteridium latiusculum (Desv.) Maxon.
Equisetum hyemale L. var. (Equiseum hyemale)
Juniperus virginiana L. (Juniperus cinerea)
Spiranthes gracilis (Bigel.) Beck.
Betula populifolia Marsh.
Rubus villosus Ait. ? Dewberry. (Rubus trivialis)
Baptisia tinctoria (L.) R. Br.
Lupinus perennis L.
Oxalis stricta L.
Oenothera biennis L.
Apocynum androsaemifolium L.
Asclepias amplexicaulis Sm.
Asclepias syriaca L.
Isanthus brachiatus (L.) BSP.

Solanum nigrum L.
Penstemon hirsutus (L.) Willd.
Lobelia inflata L.
Krigia virginica (L.) Willd.

IX. INTRODUCED SPECIES: MOSTLY WEEDS

Populus nigra L. var. italica DuRoi.	(Populus dilatata)
Ulmus campestris L.	
Rumex Acetosella L.	
Polygonum Persicaria L.	
Fagopyrum esculentum Moench.	
Agrostemma Githago L.	
Ranunculus acris L.	
Chelidonium majus L.	
Robinia Pseudo-Acacia L.	
Aesculus Hippocastanum L.	
Hypericum perforatum L.	(Hypericum perfoliatum)
Conium maculatum L.	
Ligustrum vulgare L.	
Lithospermum arvense L.	
Nepeta Cataria L.	
Prunella vulgaris L.	
Lamium amplexicaule L.	
Datura Stramonium L.	
Verbascum Thapsus L.	
Linaria vulgaris Hill.	
Veronica agrestis L.	
Tecoma radicans (L.) Juss.	(Bignonia trumpicans)
Inula Helenium L.	
Achillea Millefolium L.	
Chrysanthemum Leucanthemum L. var.	
Arctium minus Bernh.	(Arctium lappa)
Cirsium arvense (L.) Scop.	
Cirsium lanceolatum (L.) Hill.	
Taraxacum officinale Weber.	

About one-half of the remaining species are plants no longer found, so far as known, in the vicinity of Kinderhook:

Abies balsamea (L.) Mill.	(Pinus balsamea)
Lilium philadelphicum L.	
Lilium superbum L.	
Smilacina trifolia (L.) Desf.	(Convallaria trifolia)
Cypripedium arietinum R. Br.	
Habenaria flava (L.) Gray	(Orchis flava)

Habenaria orbiculata (Pursh) Torr.	
Juglans nigra L.	
Rubus setosus Bigel.	
Oxalis Acetosella L.	
Hippuris vulgaris L.	
Rhododendron maximum L.	(Azalea arborescens)
Kalmia latifolia L.	
Gaylussacia dumosa (Andr.) T. & G.	(Vaccinium dumosum)
Gaylussacia frondosa (L.) T. & G.	(Vaccinium frondosum)
Convolvulus Sepium L. var. pubescens (Gray) Fern.	(Convolvulus repens)
Houstonia caerulea L.	
Campanula americana L.	
Cirsium altissimum (L.) Spreng.	

To complete the list we have (a) five species, which, if they ever grew here, were no doubt introductions, and are not now known to grow in Kinderhook:

Taxodium distichum (L.) Richard	(Cupressus disticha)
Chamaecyparis thyoides (L.) BSP.	(Cupressus thyoides)
Belamcanda chinensis (L.) DC.	(Ixia chinensis)
Indigofera tinctoria L.	
Sida spinosa L.	

and (b) eight names which are too doubtful in their application to be made use of in this paper. They include those cases in which synonymy is obscure or in which a name seems to have been wrongly applied to a plant which grew in the area under discussion:

Convallaria latifolia
Arenaria glabra
Arenaria serphyllum
Arenaria stricta
Cerastium hirsutum
Cerastium semidecandrum
Crategus coccinea
Oenothera parviflora

CONCLUSION

Since about seven-eights of the species mentioned by Woodworth are seen to be common or locally so about Kinderhook at the present time, we may conclude that no great changes have taken place in the flora during the last century. This is borne out by the fact that numbers of species in the arbitrary habitat groupings which the writer has made above agree very well with relative numbers of species in the same habi-

tats today. The above conclusion is perhaps to be expected, since the village was settled by the Dutch about 1640, and reference to old maps and deeds shows that farm boundaries have existed, much as they are at present, for many years. The greatest single change in the aspect of the vegetation has been in the cutting of several small areas of first-growth timber, mostly White Pine and Hemlock, some of which was standing as late as 1900.

A closer study of Woodworth's list, however, seems to indicate that the northern or high-altitude elements of the flora were more pronounced formerly than now; the following selection of plants noted by Woodworth consists of those species having decidedly northern affinities, or, in this part of the Hudson Valley, typical of cold bogs or the elevations of the Taghkanic Mountain region to the eastward:

*Pinus resinosa Ait.
*Larix laricina (DuRoi) Koch
Abies balsamea (L.) Mill.
*Calla palustris L.
Lilium philadelphicum L.
Smilacina trifolia (L.) Desf.
Cypripedium arietinum R. Br.
Habenaria flava (L.) Gray
Habenaria orbiculata (Pursh) Torr.
*Coptis trifolia (L.) Salisb.
Rubus setosus Bigel.
Oxalis Acetosella L.
*Acer pennsylvanicum L.
*Epilobium angustifolium L.
Hippuris vulgaris L.
*Cornus canadensis L.
Kalmia latifolia L.
*Kalmia angustifolia L.
*Kalmia polifolia Wang.
*Menyanthes trifoliata L.
Houstonia caerulea L.

At the present time none of the above species is even locally common near Kinderhook; the ten marked with a star are rare in the vicinity and the rest are unknown. The ten species now growing here are known from only two to three stations at most. Accordingly it seems probable that the plants in the above short list occupied a somewhat more prominent place in the flora of a hundred years ago than they do now, if they were all to be recorded in a catalogue which is made up mostly of fairly common

plants. These species may have found conditions favorable to their growth in the deeper, colder forests of which only the stumps remain; forests which still persist to some extent in the more thinly settled portions of Columbia and Rensselaer counties, and in which are found in more or less abundance most of the plants noted above.

It also seems worth while to add a short list of species, now rare or unknown in the vicinity of Kinderhook, which may have been frequent or occasional in their occurrence at the time of Woodworth. This is largely speculative, but is in part supported by ranges of species as published in the manuals, and by references to various species by authors of local floras such as Hoffmann, Hoysradt, Stebbins, Wright and Hall, and others:

Uvularia grandiflora Sm.
Lilium superbum L.
Epipactis pubescens (Willd.) A. A. Eaton
Juglans nigra L.
Lupinus perennis L.
Nyssa sylvatica Marsh.
Rhododendron maximum L.
Gaylussacia dumosa (Andr.) T. & G.
Gaylussacia frondosa (L.) T. & G.
Convolvulus Sepium L. var. pubescens (Gray) Fernald.
Isanthus brachiatus (L.) BSP.
Campanula americana L.
Cirsium altissimum (L.) Spreng.

No effort has been spared to prevent errors in transcribing the above catalogues, but some have undoubtedly crept in. While such an article as the present one is largely of local interest, it is felt that it shows the general trend of plant associations well enough to merit general publication. In the preparation of the manuscript the writer has availed himself of the help of several friends, and he wishes especially to thank Dr. Homer D. House, the State Botanist of New York, and Dr. John M. Fogg, of the University of Pennsylvania, for their generous assistance at all times.

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